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SECOND NOTE ON CERTAIN PECULIAR FUNGUS-PARASITES OF LIVING INSECTS[1]

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(WITH PLATES I–V)

Although the examination of mycological novelties possesses a certain fascination, it may have its drawbacks, since in the present, as in numerous other instances that might be mentioned, their interest may be neutralized to a considerable extent by their very novelty, which may be of such a nature as to make it impossible to assign them a satisfactory position among their fellows, or to arrive at any reasonable conclusion as to the true significance of their characteristics. Although from the point of view of the systematic mycologist, and for his greater peace of mind, Nature might well have been better employed than in elaborating organisms which, as far as one can see, are in one way or another interlopers in the scheme of organic life, it seems desirable to assemble them as they appear, since the inevitable accessions to their numbers may ultimately be expected to supply, in a majority of cases, some reasonable explanation of their characteristics, which will make it possible to distribute them satisfactorily in their mycological pigeonholes.

This situation seems to be well illustrated by many of the forms included in these parasites of living insects, which if their isolation were less striking would claim more attention, and have to be put aside until the discovery of similar and related forms

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4053

may serve to make clear their significance. The Laboulbeniales, being a microcosm in themselves, need no apologist; since, despite their unsolved origin, their general position in the fungus series is perfectly clear, except possibly to a few Brefeldians; and, once they have originated, their extraordinary development is quite intelligible. With our present knowledge as a guide, however, the same can hardly be said of the other external fungus-parasites of living insects included in this and in my previous paper[2] on the same subject. Even in the case of genera like *Muiogone* and *Muiaria*, the similarity of which to well known types is manifest, it would be very difficult satisfactorily to explain their manifestly unsuccessful mode of life, the disadvantages of which seem clearly indicated by their rarity, both as regards individuals and species. While such forms may be looked upon rather as outcasts from their proper groups, however, there are others, like *Coreomycetopsis*, the Thaxteriolae, and Enterobryae, which must be regarded as essentially isolated.

This assemblage of species has been obtained from various parts of the world, on insects belonging to numerous different genera of the Coleoptera, Diptera, Orthoptera, and Neuroptera, the most curious forms having been found on Termites, already a classic ground for the parisitologist. Although the first, *Cantharosphaeria*, which is a true ascomycete, may perhaps prove to be, in a sense, saprophytic, with no very definite relation to the vital activities of its host, this can hardly be said of any of the others, the life of which is evidently thus conditioned. *Termitaria*, *Muiogone*, *Muiaria*, and *Aposporella* belong to the Fungi Imperfecti; the first referable in an artificial way to the Leptostromaceae, but quite isolated in its characters; the last, one of the Mucedineae, belonging to a group which includes a number of forms as yet unpublished, having a similar mode of life, and characterized by an absence of differentiated spores, among which the species herewith illustrated is, in some respects, the most striking. *Muiogone* and *Muiaria*, of which species have been previously described, belong to the Dematiae. The position of all the remaining forms, however, is problematical, and, although from its cytological characters

[2] Bot. Gaz. 58:235–253. *pls. 16–19.* 1914.

Enterobryus may be assumed to belong to the Phycomycetes, evident affinities with other members of this class are lacking.

Cantharosphaeria, nov. gen.—Perithecia superficial, scattered, subdimidiate, membranaceous, ostiolate, the ostiole surrounded by a tuft of hairs. Asci 8-spored, aparaphysate; spores hyalodidymous.

Cantharosphaeria chilensis, nov. sp. (figs. 1–5).—Perithecia associated with a rather scanty mycelium of thick-walled, brown, branching hyphae; subhemispherical, blackish brown, slightly roughened, seated on the chitinous integument among the bristles of the host, about 70–80 μ by 40–45 μ; the apical hairs usually closely aggregated about the ostiole, 35×2.5–3 μ, about a dozen in number, rather coarse, irregular, simple, and brown. Asci rather short and stout, sporiferous to the small, short, rather abruptly narrower base, distally rounded, 28×10 μ; ascospores hyaline, the septum median with a very slight constriction, or the basal segment slightly shorter and narrower, subdistichous, 12–14×4.5–5 μ.

On the elytra, legs, etc., of a cucujid beetle found in decaying vegetable material, Corral, Chile.

A single specimen of the peculiar host which bears this fungus was collected in decaying vegetable material at Corral. It is evidently a beetle of somewhat unclean habits, since it bears numerous stalked mites, and is covered with a thin film of foreign matter such as one often sees on species of Silphidae. The perithecia are numerous, and appear under a hand lens as black points scattered irregularly over the surface (fig. 1), the individual perithecia nestling among the peculiar hooked spines of the host as shown in fig. 3, and associated with a variably developed, brown, thin mycelium of thick-walled branching hyphae (fig. 2), which can hardly be called a byssus. The terminal hairs eventually break off, exposing the evident ostiole in old specimens. The surface is slightly roughened, and occasionally a hair may be seen projecting apart from the group about the ostiole.

I have concluded with reluctance to apply a new generic name to this type, yet its close relationship to other genera does not seem at all clear. It probably is not truly entomogenous, deriving its nutriment directly from the living insect, as in all the other types herewith described; and it is not unlikely that it may obtain its necessary materials from the film of foreign matter which covers the surface of its host.

Termitaria, nov. gen.—General habit disciform, applanate or hysterioid, orbicular or variously elongated according to position of growth, sessile; consisting of a basal pseudocellular layer,

from which firmly coherent, simple, parallel sporogenous elements arise vertically, forming an even hymenial surface, the contents of the upper portion of each element becoming separated to form a single row of endogenous, simple, hyaline spores, which are discharged through a terminal perforation; the peripheral elements sterile, dark, indurated, forming a well defined rim or exciple; the margin in contact with the substratum slightly spreading and lichenoid.

This structure, which characterizes the mature condition of this very remarkable type, two species of which have been examined from living Termites, appears to be a secondary development, which results from the vertical proliferation of a primary stage similar to that represented in figs. 6 and 13. This primary condition may be more or less elongated or orbicular, varying to some extent according to the position of growth; it is formed by a continuous layer of slightly brownish cells, the whole reducible to a copiously branched and septate filament, the branches of which are in lateral contact, the ultimate branchlets forming a radiate lichenoid margin. As the cells mature and enlarge, there may be more or less displacement, as a result of which the fundamental arrangement of the cells in branching filaments may be obscured or obliterated. The general appearance of this stage, as represented in the figures cited, recalls that of some species of *Asterina* or of a young *Aglaozonia* or some species of *Coleochaete*, the resemblance to the latter being rendered more realistic by the presence of the projecting bristles of the host, which are completely surrounded by the advancing margin and are left projecting from the thallus without displacement. Of the cells which form this primary incrusting layer, many usually become characteristically modified (fig. 13), assuming the appearance of chlamydospores, which are clearly differentiated from the unmodified cells about them by their greater size, thicker walls, more rounded outline, and deep brown color. Whether these bodies are ever separated and become functional spores it has not been possible to determine, although various instances have been seen in which they appear to have been dislodged.

The preliminary stage just described has been seen in only a few cases, and a complete series, showing the transition from this to the

mature condition, has not been obtained. From such young specimens as have been examined, however, it is evident that a proliferation takes place over the surface of the primary stage, which results in the development of the structures distinguishing the genus. The primary thallus thus forms a thin substratum, more or less firmly coherent to the surface of the host, on which the secondary stage is seated, and which is clearly distinguishable both in crushed specimens and in sections; the brown chlamydospore-like cells persisting *in situ*, singly or in groups.

A section of the mature fungus, which under a hand lens has the appearance of a black *Hysterium* when growing on the legs (fig. 7), or of a small discomycete with pale hymenium and black margin on other portions of the host (figs. 8, 9), shows a differentiation into several distinct regions. The first is a thin dark layer of cells, in which many or few of the chlamydospore-like bodies may be visible at intervals, and which, in a favorable section, may include the primary attachment of the fungus, an indentation, associated with a group of dark cells (fig. 14) opposite which the hypertrophied cells of the host are usually somewhat brownish. No indication has been seen of any actual penetration of the parasite through the integument of the host; but these primary attachments are readily distinguished, and usually appear as a limited dark area which shows through the sporogenous region when the fungus is viewed vertically, as in fig. 9.

Above this primary layer, and derived from it by vertical proliferation, is a region of irregularly polygonal, hyaline cells, the origin of which, as components of a series of branching hyphae, is obscured or quite obliterated through unequal growth and mutual pressure, and is only indicated by a tendency of the lower cells to retain an arrangement in vertical rows. The thickness of this region is somewhat variable, the cells becoming smaller and numerous above; the uppermost giving rise to the straight, erect, tubular, and apparently always simple filaments which compose the sporogenous layer or region. In this layer, which is four or five times as thick as that from which it is derived, two regions are again recognizable, the limits of which may be very clearly indicated. In the lower of these regions the continuous protoplasmic content

of the individual filaments is more dense, and stains more deeply; although this distinction becomes less marked in older individuals, in which, however, the limits of the zone may be even more clearly marked (fig. 14) through the often deep distal suffusion of the walls. Above this line of demarcation in the upper zone, which simulates an ascigerous hymenium, the walls of the upright tubes become somewhat thicker, gelatinous, and tenaciously coherent; while the protoplasm of each is segmented to form a series of short cylindrical spores, which is constantly renewed and pushed upward by the activities of the denser contents of the lower zone. The spores separate from one another as they pass into a somewhat paler region below the surface (fig. 12), becoming slightly rounded at the extremities, with a few sometimes conspicuous granules. The discharge of these endogenous spores through the terminal perforation of the tube has not actually been observed, but is doubtless effected with some violence, the thickened walls around the opening, and the mutual pressure of the gelatinous hymenial elements, combined with the constant pressure from below, affording an effective mechanism for this purpose. The dimensions of the sporogenous elements are very small, and owing to their gelatinous nature it is usually only with the greatest difficulty that the limits of single tubes can be distinguished with exactness in sections, or in crushed specimens; in fact no outlines are clearly defined in this region, and even after staining, the minute spores are often recognized with difficulty under high magnifications. The spores do not seem to possess a wall, or if they have one it is so thin as to be hardly demonstrable. Isolated spores are seldom recognizable on the hymenial surface of healthy individuals, but when the host is confined for a considerable period under somewhat unfavorable conditions, the normal discharge seems to be interfered with, and it may become whitish with a coating of extruded spores.

At the periphery of the hymenium the sporogenous tubes become sterile, thickened, and blackened, forming the inner portion of the well defined, deep black-brown rim or exciple; while a narrow, radiate, lichenoid margin spreads out externally from the base (figs. 7, 8), in close contact with the surface of the host.

As far as can be determined from the series of specimens examined, there seems to be no continuous increase of the fungus in diameter after the original proliferation of the primary stage, which gives rise to the sporogenous region. This is indicated by the fact that this region, as soon as spore formation has begun, is surrounded completely by sterile indurated structures, incapable of radial extension, and also by the fact that the bristles of the host, which are surrounded by the filaments of the preliminary stage, are not bent down as by an advancing margin, but retain their normal position, and may even be seen projecting beyond the hymenial surface of mature individuals, as in fig. 10.

Although each individual must produce an enormous number of spores, this very curious type does not appear to have been very successful in propagating itself effectively; for although its hosts are densely gregarious and live under conditions which should be very favorable for the communication and development of such parasites, hardly more than 1 per cent of the individuals in an infected nest appear to bear the fungus. SNYDER, who was the first to observe the type species of this parasite and to whom I am greatly indebted for the original material examined, informs me that he has found this ratio of infection more or less constant in material from a number of different sources, and SMULGAN, who has also kindly communicated material from the Boston region, makes a similar estimate. In the case of the second species, described from the Island of Grenada, I have also found almost exactly the same percentage of diseased individuals among the several thousand hosts examined.

It does not appear seriously to inconvenience the insect on which it grows, and the only indication of injury is a slight browning of the tissue immediately opposite the primary attachment, as shown in fig. 14, although all the cells of the tissue lying immediately below the integument are hypertrophied, wherever the fungus is in contact with the host, often assuming a rather regular palisade-like structure, similar to that shown in fig. 10. It is most conspicuous when growing on the abdomen (fig. 9), where it is likely to assume a more regular and rounded form, being suborbicular, or more often transversely elongated, with an even or sometimes

slightly irregular outline (fig. 8); but it may also attack the thorax and head, and very often occurs on the legs, where it assumes a long fusiform outline, like that of a hysterium (fig. 7). Individuals of the latter type which have developed on the tibia, from a point of infection near the terminal claws, are sometimes connected with the original point of infection by a narrow primary thallus which remains unchanged on the intervening joints of the leg, spreading out and producing the secondary stage only on the broader and more nutritious tibia.

The relationships of this fungus are quite obscure. The general characters of its primary stage might suggest a resemblance to some Asterinae, or to a similar incrusting type. Its mature condition, however, evidently a Fungus Imperfectus, seems to give it a formal place among the Leptostromaceae. Its method of sporulation, which in certain respects recalls that of the Chalareae, or of *Sporochisma* or *Endoconidium* among the Hyphomycetes, would seem to make its position in this group an isolated one.

Termitaria Snyderi, nov. sp. (figs. 13–17).—Characters of the genus. Sporogenous filaments with blunt or flat perforate terminations forming an even hymenium. Total thickness of sporodochium 70–80 μ; basal region including primary thallus 18–20 μ; sporogenous region 55–65 μ, the upper zone 25–28 μ; sporogenous hyphae a little over 3 μ in diameter; free spores about $3.5 \times 2\ \mu$. Sporodochium on abdomen 400×400–$1000\ \mu$.

On workers and soldiers of *Reticulitermes flavipes* and *R. virginicus*, Washington, D.C., the former also vicinity of Boston. On *Reticulitermes*, nov. sp., California. On *R. lucifugus*, Sardinia. A specimen on *Rhinotermes marginalis* from Turkeit, British Guiana, kindly communicated by NATHAN BANKS, does not appear to differ from the type. The material, however, is too scanty for a satisfactory determination.

This form, which is evidently widely distributed, was first observed by SNYDER, to whom I take pleasure in dedicating it, and who has figured its gross appearance in *fig. 9c*, p. 29, Bull. 94, Part II, Bureau of Entomology. It was first sent me at his request by A. D. HOPKINS with an inquiry as to its possible fungus nature, and has also been brought to my laboratory by both SNYDER and SMULGAN from the Boston region.

Termitaria coronata, nov. sp. (figs. 6–12).—Sporogenous hyphae bearing distally a crown of several, more often four, brown-tipped,

minute, pointed prolongations which form a minutely echinulate hymenial surface. Total thickness 80–100 μ; basal region including primary thallus 16–20 μ; sporogenous region 70–78 μ, its upper zone 45–50 μ; sporogenous hyphae ×2.5 μ; spores about 3.5×2 μ.

On *Eutermes morio* var. *St. Luciae*, Grand Etang, Grenada, B.W.I.

The two species described, although hardly distinguishable in general appearance, seem to be clearly separated by the minute, dark, toothlike projections which terminate the sporogenous hyphae in *T. coronata*, and give to the surface of its hymenium a finely punctate appearance which is suggested with sufficient exactness by the stipple in figs. 7, 8, and, under a high power, has the appearance represented in fig. 11. In *T. Snyderi*, on the other hand, the corresponding terminations are unarmed, blunt, and when viewed from above show clearly their rounded ends, slightly polygonal from mutual pressure, and having a readily distinguishable central pore (fig. 15).

The dimensions of the two species, although they are variable in either case, are usually somewhat different; the sporogenous hyphae of *T. coronata* being slightly larger in diameter and length, the relative length of the portion included in the upper zone always being greater. The extremities of these hyphae in this species are quite hyaline and gelatinous, and so tenaciously coherent that I have been unable either to distinguish clearly the terminal pore, or to trace definitely to their bases the characteristic terminal toothlike prolongations shown from above in fig. 11, and laterally in fig. 12. While within the tubes the spores are evidently compressed, and when free increase in diameter, becoming more rounded at the extremities.

Muiogone Medusae, nov. sp. (figs. 18–25).—Sporophores about as long as the spores, rather closely septate, densely crowded so that the whole forms a cushion-like mass on the surface of the host. Spores somewhat irregular, subpyriform, distinctly broader distally, uniform pale dirty brownish, consisting of 10–12, more often 11, more or less regular tiers, the numerous cells of which may be slightly misplaced, those of the basal and distal tiers often slightly larger than the rest, but otherwise indistinguishable from them; a variable number of the distal ones proliferating while still quite young to form a terminal group of tapering, spirally coiled, simple or sometimes once branched appendages which may bear minute secondary spores at their pointed extremities or on short, pointed, subterminal branchlets. Spores 38–45×20–24 μ; terminal appendages 28–30×4 μ at base; stalks, maximum, 38×6 μ.

On the under surface of the abdomen of *Chromopterus* sp., Kamerun, West Africa.

The fly on which this curious form grows is closely related to, if not identical with, *C. delicatulum*, which bears the type species of *Muiogone*. It is quite unexpected that a genus, which has not been seen on any of the numberless genera and species of flies from the tropics that I have examined, should be represented on the same, or on two at least very closely related hosts, by two such clearly distinguished species, of which but one specimen in each instance is known. The present form, although it has exactly the same gross habit, and occurs in the same position on the underside of the abdomen, is clearly distinguished by its uniform pale brown color, the sometimes total absence of any suggestion of a distinction between basal distal and median regions in the somewhat more irregular cell-tiers, and especially in the terminal, spiral, septate, tapering appendages which replace the short spines of the type species, and the resemblance of which to a Gorgon's head has suggested the specific name. These appendages are not formed after the spore has matured, but begin to appear some time before it has attained its full size (fig. 22), although most of the cell divisions have been completed. There is some variation in the spirals, which may be quite regular, or rather indeterminate; and although they usually end in a pointed apex, they may be somewhat blunt. The minute secondary spores are only recognizable here and there in spores which are still *in situ* (figs. 23, 24). The primary spores become detached, together with an adherent portion of the stalk, and there seems to be no definite mechanism for abjunction. After having been broken thus, the base of the stalk, which remains in position, proliferates as shown in figs. 18 and 19, so that the spore mass is constantly renewed. Owing to the presence of the terminal appendages, as well as the lack of any clear differentiation between the basal, terminal, and middle regions, the original generic diagnosis should be slightly modified.

Muiaria curvata, nov. sp. (figs. 26, 27).—Sporophores and sterile elements springing in small numbers from a compact blackened base. The spores 2 or 3 in a group; the stalks short, of 5 or 6 cells; the termination rather slender, strongly curved, or characteristically recurved distally; the body of the spore rather clearly distinguished, marked by large, very irregular, more or less longitudinal patches, separated by fine light lines and slightly roughened, the 4 tiers of functional cells rather well defined, including the broadest portion and with convex margins, the cells relatively large; the lower of the 3 cells above, and usually the upper of the 2 or sometimes 3 cells below, showing one longitudinal septum; rather pale yellowish olive brown, the concave side of the termina-

tion darker. Body of spore about 52–60×20 μ, the termination 65–70×8, the stalk 50–65 μ.

On the superior tip of abdomen and wing of a small drosophilid fly, Bocas del Toro, Panama (*Rorer*), no. 2525.

This species is perhaps more nearly allied to *M. repens* and the succeeding species. From the former it is distinguished by its 4 clearly defined functional tiers, its much longer, slender, curved termination, and the absence of an appendage from the stalk; while from the latter it differs in its smaller size and quite differently shaped spores. One other American species, also allied to *M. repens*, is known from Trinidad, but more material is desirable before it can be described.

Muiaria fasciculata, nov. sp. (figs. 28, 29).—Tufts compact, the spores and rather numerous sterile elements arising from a usually well defined black base; the stalks relatively long, the termination relatively slender, and usually curved, but somewhat variable, the body of the spore blackish brown, roughened by very irregula intricate darker markings, the 4 functional tiers well defined, relatively short, paler, and rather abruptly narrower than the cells immediately below, of which two are usually flattened, and one or both longitudinally septate; the cells above 3 or 4, the lower usually septate. Body of spore 85–100×24–28 μ, the stalk 100–210 μ, the distal termination 50–64×8 μ.

On a dull brown drosophilid fly, no. 2749, Kamerun, West Africa.

This species occurs on the wings, especially on the veins, of its host, a rather large smoky drosophilid, several specimens of which have been found to bear it. It is clearly separated from the preceding species by its greater size and different shape. From *M. Lonchaeana*, which is the only other form with which it might be confused, it is distinguished by the fact that the stalk and distal portion of the spore are not roughened, as well as by its different form.

Aposporella, nov. gen.—Mucedinaceous, aposporous, entomogenous, a well defined septate axis attached by a blackened foot and bearing short branches at the septa, which separate short undifferentiated segments distally that are constantly renewed.

Aposporella elegans, nov. sp. (figs. 30, 31).—Axis stout, erect, straight, or but slightly curved, tapering, simple, the superposed cells but slightly longer than broad, hyaline, the black foot clearly defined; the branches short, simple, one to several in an irregular whorl from all but the terminal cells; somewhat appressed, or but

slightly divergent, externally edged with blackish brown, except at the tips; the termination of the axis hyaline, slender, projecting, without branches. Total length 200–540×8 μ near the base, where the cells are 10–14 μ long. Branches before breaking, longer, 50×4.5 μ.

On the wings of a small fly, Kamerun, West Africa, no. 2645.

Sufficient material of this graceful form has been examined to convince me that the individuals figured are fully matured, and that there is no abjunction of definitely differentiated spores, a character in which it agrees with a small assemblage of aposporous Hyphomycetes of which I have half a dozen or more species from Africa and the East and West Indies that are reserved for future consideration, and to which reference was made in my former paper (*loc. cit.*, p. 237).

In this connection it may be mentioned that SPEGAZZINI has recently (*loc. cit.*) described certain Argentine forms which he refers to *Chantransiopsis*, several dubious examples of which, from Africa and the West Indies, I have myself encountered since the genus was established. One of the forms described by SPEGAZZINI under this name, but which seems to me not closely related to it, is a problematical type which I have examined on Forficulae and Staphylinidae from the East and West Indies, and from Argentina. It consists of a deep brown, several-septate body, resembling a spore of *Hendersonia* for example, elliptical in outline, convex above, and flat below, where it is in contact with the substratum. From usually the end cells of this body are developed a group of simple, straight, septate, hyaline hyphae. I have never seen these hyphae producing anything in the nature of a spore, although SPEGAZZINI figures one which appears to be developing as a terminal proliferation. The position and history of this singular form must, I think, remain somewhat doubtful. Although I have examined hosts well covered with the brown, septate, primary structures described, I have never seen any that suggested their origin and development, which has led me to suspect that they might after all prove to be spores of some fungus, not entomogenous, which develop in situations frequented by the hosts, and adhere to them as the spores of agarics and other Basidiomycetes adhere to Endomychidae and Erotylidae. The peculiar form of these bodies, however, and their almost universal germination in the manner described, make such a supposition doubtful.

In the same paper SPEGAZZINI has described a true species of *Chantransiopsis* which he refers to a new subgenus *Asteronycha*, based on a slight difference in the form of its dark attachment. In his comments on these plants he appears to have misunderstood my expressed opinion in regard to their position, or at least overlooked my statement, on page 230 of my former paper, that the genus "comprises species belonging to the Hyphomycetes," and on page 247, where I mention, in connection with the suggestion that they may be related

to the Florideae or the Laboulbeniales, that "there seems not the most remote possibility that such is actually the case."

Coreomycetopsis, nov. gen.—Axis consisting of an indeterminate series of superposed cells, the basal one modified to form a characteristic foot attached to the host; the distal portion transformed into a sporogonium, its successive septa being destroyed, or absorbed, through the upgrowth of sporophores which spring endogenously from numerous divisions of an intercalary cell, and abjoint terminally simple hyaline spores; which, after being set free in the sporogonium, are discharged through a terminal perforation.

Coreomycetopsis oedipus, nov. sp. (figs. 32, 36).—Nearly hyaline or faintly yellowish, the foot large, strongly concave externally, pointed below, its insertion flattened, wholly concolorous with the remaining cells. Axis usually bent strongly outward above the foot, consisting of 10–15 cells, including the latter; the sixth or seventh from the apex becoming proliferous, after dividing to form a central subpyriform cell and numerous small lateral ones, which are obliquely separated, and grow up through the lumina of the 5 or 6 cells above, abjointing terminally long oval spores somewhat pointed at the base; the cells above, and including the proliferous cell, transformed into a straight symmetrical sporogonium, clearly differentiated, and fusiform or obclavate in outline, broader than the 4–6 subequal stalk-cells which connect it with the foot. Total length 100–135 μ. Sporogonium 45–60 $\times$ 12–15 μ; stalk 10 μ; foot 25 $\times$ 12–15 μ; spores 8–9 $\times$ 2–2.5 μ.

On the tips of the legs of *Eutermes morio* var. *St. Luciae*, Grand Etang, Grenada.

This form is usually solitary, attached to the terminal joints of the legs, and from its pale color is not readily seen, although it is larger than many Laboulbeniales. Its remarkable analogy to *Coreomyces* is suggested by the generic name selected, and if the spores were formed in asci, instead of being abjointed, it would be placed near that genus, since the history of development of its sporogonium, and that of the perithecium in *Coreomyces*, is remarkably similar. The destruction of the upper cells to form the common cavity of the sporogonium does not appear to be due wholly, at least, to the upward pressure of the traversing sporogenous elements, since these cells evidently begin to disorganize as soon as the first intercalary divisions appear

(figs. 33, 35), and the uppermost septa are not reached by the sporiferous filaments themselves.

In general appearance this plant is so like some of the Laboulbeniales that at first I was inclined to believe that it might prove to be the male individual of some ascigerous form characterized by an entirely new type of antheridial structure. Its development, however, is so widely different from anything hitherto known among the Laboulbeniales that there seems to be no good reason to suppose, in the present condition of our knowledge of such parasites, that it is even remotely related to them, an opinion which is supported by the fact that a careful search has failed to bring to light individuals of a different nature. Since, however, its relation to other types of fungi is equally problematical, it will have to await further developments in the limbo "genera incertae sedis," in company with its companion *Laboulbeniopsis* on the same host described below, to which, despite a superficial similarity, it seems also quite unrelated.

THAXTERIOLA Spegazzini.—This name has been used by SPEGAZZINI (Ann. Soc. Nat. Arg. **85**:314) in a paper entitled "Observaciones Microbiôlógicas," under the caption "Anforomorfideas Argentinas," to designate a series of very minute and simple forms common on various insects, especially Staphylinidae, two species of which were figured in my former paper (*loc. cit.*, figs. 30–31), and referred to in the text (p. 250), no name being used to designate them, owing to a lack of any complete knowledge of their history and to their general insignificance. These organisms consist primarily of two cells, the lower attached by a well defined black foot, corresponding entirely with that of most Laboulbeniales; while the upper, having become prolonged to form a necklike termination, and having previously separated, at its base, a smaller cell from which it is more often obliquely distinguished, produces minute, naked, sporelike bodies formed in a single series and discharged through the perforate extremity. These plants closely resemble male individuals of *Amorphomyces*, among the Laboulbeniales; but their occurrence in large numbers, and under no other form, precludes the possibility that they may be conditions, or stages, of any member of this family. Whether, as in the sperm cells of *Amorphomyces*, the spores produced by *Thaxteriola* are formed continuously, as seems most probable, or cease to be produced after the protoplasm of the sporogenic cell has been exhausted, I have not been able to determine satisfactorily. SPEGAZZINI, how-

ever, since in his generic diagnosis he says that "articulum supremum sporis amoeboidëis repletum," appears to assume that the latter supposition is correct. I have not seen the sporogonium "sporis repletum," and the usual appearance of the individuals examined has been that shown in figs. 37, 38, the spores occupying the upper portion of the cell and being arranged in a single series, not irregularly disposed as in SPEGAZZINI'S fig. 5, and similar to that which occurs in the closely related *Endosporella* described later. It should be pointed out, however, that in the genus *Laboulbeniopsis*, a description of which follows, and which appears to be otherwise similar, a simultaneous formation of irregularly distributed spores appears to take place.

In order to facilitate a direct comparison between this type and the others here considered, I append a description of a Javan form that seems sufficiently distinct for ready recognition. Since they are now known to occur on such diverse hosts as gamasid mites, Forficulae, Hemiptera, and Coleoptera, it may be assumed that numerous species of this group exist, none of them too well defined; and it is probable that by the time systematists have finished with them, posterity will have become burdened with a horde of these uninteresting little plants.

Thaxteriola nigromarginata, nov. sp. (figs. 37, 38).—Subsigmoid, pale brownish, except the clear hyaline base and apex; the distal half edged with deep blackish brown, the suffusion broader toward the middle. The basal cell including half the total length; its extremity slightly broader than the distal half, the lower cell of which is very obliquely distinguished from the upper, and is distinctly concave on its longer side, being also free from any blackish suffusion. Total length 62–68 μ; greatest width (distal portion of basal cell) 8–8.5 μ.

On the hairs of a minute staphylinid, no. 2082, Samarang, Java.

I am indebted to JACOBSON for the host bearing this species, which was found among a few beetles collected at Samarang. It seems sufficiently well distinguished from the types usually common on Staphylinidae by its slightly sigmoid outline, more slender distal half, the lower cell of which is distinctly concave on one side when viewed laterally, by the very oblique separation between this and the sporogenous cell, and by the well defined and rather clearly circumscribed black marginal suffusion of the latter, which contrasts strongly with the adjacent hyaline areas.

Two species of this genus have been described by SPEGAZZINI, to one of which, *T. infuscata*, he refers the form represented in fig. 31 of my former paper, which represents an individual found on *Labia minor* in Cambridge, and is distinguished by the fact that the two upper cells are not separated by an oblique septum. His second species, *T. subhyalina*, which occurs on *Aphodius*, is said to be distinguished by the fact that it is always hyaline, the neck more strongly curved, and the basal cell relatively shorter.

A second genus of a similarly nondescript type has been named *Entomocosma* by the same author (*loc. cit.*, fig. 7, pp. 312–315). Although possibly related to the present genus, its essential characters are not at all clear. It seems in some respects similar to a problematical type, of which I have material collected at Waverly, Massachusetts, in 1893, on *Tachinus pallipes*, and which I have not subsequently observed.

It is to my mind very doubtful whether any close relationship exists between these genera of "Thaxteriolae," to which two others are added below, and the "Anforomorfas" with which SPEGAZZINI associates them, and of which the *Amphoromorpha entomophila* of my former paper may be taken as the type. As in the case of *Coreomycetopsis*, however, their relationships to other groups are equally obscure, and they must remain among the "genera incertae sedis" until the discovery of further types which may possibly throw some light on their affinities.

Endosporella, nov. gen.—Axis consisting of 4 superposed cells, the basal attached by a well differentiated foot; the terminal one spinose, separating uniseriate endospores distally, which escape through a terminal pore.

Endosporella Diopsidis, nov. sp. (figs. 39–41).—Foot small, black, and pointed; basal cell abruptly narrower and hyaline below, the upper half becoming much broader and somewhat inflated distally, obliquely suffused with blackish brown. Second and third cells much shorter, subequal, or the upper usually slightly longer and broader; terminal cell a sporogonium, sometimes as long as the rest of the individual, deeply tinged with blackish brown, except the hyaline tip, which is primarily spinose and becomes perforate, the upper half or more becoming filled with a simple

series of flattened superposed naked spores, which are successively separated from the protoplasmic mass below. Apex opening irregularly beside the large terminal spine, which seldom persists. Total length 100–150×10–13 μ. Sporogonium 50–60×10–12 μ.

On the terminal claws of the legs of *Diopsis* sp., nos. 2716, 2717, Kamerun, West Africa.

This type is most nearly allied to *Thaxteriola*, from which it differs in being 4-celled, the sporogonium having no differentiated efferent neck, and discharging broad flat spores. A majority of the individuals examined are comparatively young, and only a few are beginning to form spores, so that in this instance it is also impossible to say whether sporulation is a continuous process or ceases after all the primary contents has been used.

Laboulbeniopsis, nov. gen.—Axis simple, consisting of a differentiated foot, a 2-celled stalk, and a well defined terminal sporogonium, at the base of which two cells are distinguished, the rest of the cavity being filled with numerous minute hyaline spores, which escape through a terminal perforation.

Laboulbeniopsis Termitarius, nov. sp. (figs. 42, 43).—Foot and sporogonium pale brownish, the stalk nearly hyaline. Foot large, externally strongly convex, a portion of its flat insertion deeply blackened, more or less pointed below; the stalk much narrower, its upper cell shorter and broader than the lower. Sporogonium as long as or longer than the stalk, straight, subsymmetrical, slightly inflated below, tapering distally to the rather broad, slightly flaring terminal pore, which is subtended by a scarcely distinguishable constriction; the basal cells occupying the lower fourth or less of the cavity, lying side by side, one slightly larger than the other. Total length 100–130 μ; sporogonium 45–50×12 μ; stalk ×8–10 μ; foot 25×12 μ; spores 3.5–4×2.5 μ.

On tips of legs of *Eutermes morio* var. *St. Luciae*, Grand Etang, Grenada, B.W.I.

This form occurs very rarely, associated with *Coreomycetopsis*, of which it was at first believed to be a stage or condition. The two, however, do not seem to be related, although their general appearance is so similar. There is not sufficient material available to determine the complete history of its sporulation. As far as can be determined from the material available, the spores develop simultaneously, filling the whole cavity of the sporogonium above its two basal cells, and there is no evidence in the specimens examined that successive periods of spore-formation occur, after the first are discharged.

In several cases the sporogonium has emptied itself, leaving a few residual spores, and in such individuals the basal cells, as shown in fig. 42, are already more or less disorganized, while the spores may be considerably swollen and rounded, measuring even as much as $6\times3.5\ \mu$, having surrounded themselves with more or less evident walls.

Despite the apparently simultaneous formation of the spores, however, and their irregular distribution throughout the cavity of the sporogonium, it seems best, at least provisionally, to associate this type with *Thaxteriola* and *Endosporella* in a group of "Thaxteriolae," to which the genus *Entomocosma* Speg. may possibly be added.

AMPHOROMORPHA Thaxter.—The type of this genus, *A. entomophila*, was described and figured in my previous paper (*loc. cit.*, p. 251, figs. 26–28), having been observed on species of *Labia* and *Diochus* from the Philippines. It has since been noticed on a carabid allied to *Platynus* from Jamaica, on a species of *Pachyteles* from Verdant Vale, Arima, Trinidad, and on a host allied to *Ardistomis* from Hayti. Although the specimens obtained from these sources correspond in all respects with the original types, the more abundant material thus made available furnishes certain additional information which is of interest and tends to harmonize the characters of this species with those of other related forms which are not distinguished by the same striking specific peculiarities.

An examination of specimens removed *in toto*, so as to include the whole individual, including its attachment, and viewed anteriorly or posteriorly, shows that the foot, which, when viewed sidewise, usually appears to be black and quite opaque and would naturally be assumed to correspond to that of most Laboulbeniales, or of the Thaxteriolae, is of quite a different nature. This is due to the fact that its main mass consists of a secretion which spreads over the surface of the host, and, when viewed in the position indicated, is translucent, and may be transparent enough to show the actual termination of the organism. This termination is very clearly a short, abruptly distinguished rhizoid (fig. 45), which is held firmly against the host by the indurated secretion just mentioned, and suggests the somewhat analogous rhizoidal attachments of some of the Rhizideae among the Chytridiales.

An identical condition is seen in the other species of this type, two of which are illustrated in figs. 44 and 46. The character of

the wall, its general appearance and texture, are also very like some of the Chytridiales, and unlike that of the Thaxteriolae, with which I was at first inclined to associate them. My present impression, however, is that they have little if any relationship to one another. There seems no reason to believe that they are not, like the Chytridiales, strictly unicellular. Although their developmental history is not, as yet, exactly known, it seems probable, from an examination of the stages available, that the sequence of events may be very similar to that seen in the temporary sporangia of *Cladochytrium Alismatis*, for example. On the basis of this supposition the original cell may be assumed to divide completely into spores, as has been the case in the individual of *A. entomophila* (fig. 45). Figs. 26, 27, and 29 of my former paper, on the other hand, may well be interpreted as illustrating different periods in the spore discharge, which may be, in part at least, effected by pressure exerted as the result of an intrusion into the sporogonium of a new sporogenous cell, which may be assumed to fill the cavity after the spores have effected their exit, and to become transformed into another spore mass to be discharged in a similar fashion. As there is no indication that cilia are present on the spores, it is not easy to see how otherwise the sporangium could be completely emptied through so narrow an orifice. However this may be, it is evident from the condition shown in fig. 45 that the generic diagnosis must be modified, no sterile basal cell being clearly distinguished.

It is also evident, however, that the true position of this type, as well as the exact sequence of events in its development, have yet to be accurately ascertained. I should not be reluctant even to turn it over to the zoologists, although E. G. RACOVITRA, who has figured a more simple type observed on crustaceans (Arch. Zool. Exp. 1907–1908. pl. 10. fig. 26; 1908–1909. p. 272. fig. 2), speaks of it as "une Laboulbeniacea parasite." Further references of this nature, if they have occurred within the past few years, have escaped my notice, with the exception of the account given by SPEGAZZINI in the paper already cited, in which he described under the name *Amphoropsis* three species: *A. minuta* on *Hister*, said to be the same as that represented in fig. 29 of my previous paper; *A. subminuta* on *Echiaster*, represented as somewhat more pointed

and sessile; and *A. media*, which is somewhat larger and more distinctly stalked. A second genus, *Myriopodophila*, is also created, with a single species, *M. argentina*, the only basis for which appears to be a slender habit. All of these 4 species are represented in the figures as octosporic, although this character is not mentioned in the text. I should personally be reluctant to separate either of these forms from *Amphoromorpha*, and the species of *Amphoropsis* are certainly congeneric with the types illustrated in figs. 44 and 46. Since the material of the species represented in fig. 44 is sufficiently abundant and has been observed on two different genera of roaches, it seems worth while to append a description, although all the individuals examined are at the same point of development, the sporogonia being completely filled with spores.

Amphoromorpha Blattina, nov. sp. (fig. 44).—Yellowish, sessile, with a large dark foot. Form elongate oval, somewhat broader distally, the apex rounded. Spores between 50 and 100, about 5 μ in diameter. Total length of sporogonium 55–70 × 18–20 μ, exclusive of the foot, which is 18–22 × 18 μ, seen in front view.

On the axis of the antennae of a dark wingless and a pale winged blattid, nos. 2938 and 2939, Grand Etang, Grenada, B.W.I.

This species is similar to *A. media* in size, but differs in its form, its sessile habit, and its much more numerous, smaller spores. It is apparently confined to the axis of the antennae, where it grows among, but not on, the hairs. A second species inhabiting the hairs, and not the axis, was found in the same locality on a different host, and is represented in fig. 46. This form is characterized by a somewhat different shape, its smaller size, and transparent, hardly suffused, foot.

ASTREPTONEMA Hauptfleisch, Ber. Bot. Gesells. 13:83. *pl. 8.* 1895.—In a paper entitled "*Astreptonema longispora*, n.g., n. sp., eine neue Saprolegniaceae," HAUPTFLEISCH has described a peculiar organism which grows attached to the chitinized end of the rectum of *Gammarus locusta*, consisting of a simple, unicellular, multinucleate filament, attached at its base, and distally producing a series of successively formed spores, or rather of spore mother cells, within which single definitely walled spores are formed, at first uninucleate, and later containing as many as 8 nuclei. These spores are formed in large numbers and are eventually freed by

the disorganization of the mother cell walls. The filament is attached at the lower end, the wall of which is at first thickened, the thickening organizing a well developed and peculiar sucker-like structure, which forms a definite organ of attachment. The walls of the filament mother cells and spores are comparatively thin, although well defined. As the title indicates, this type was regarded by HAUPTFLEISCH as unquestionably belonging to the Saprolegniaceae, with a possible relationship to *Aphanomyces;* the mother cells, despite the absence of any signs of antheridia or of zoosporangia, being regarded as oogonia, and the contained spores as oospores, a comparison being drawn between them and the seriate oogonia, of *Saprolegnia monilifera* DeBary. The author's conception of the type is summed up in his "kurze lateinische Diagnose für diese neue Saprolegniaceae," which reads as follows: "Thallus non racemosus. Una tantummodo ovospora in ovogonio nata, quasi explens ovogonium. Ovosporae plurium nuclearium oblongae, 2–2.6×7–10 μ. Ovogonia terminalia semper simplici serie adnexa, aliud alii, non transfusa. Sporangia incognita. Antheridia desunt." SACCARDO in the *Sylloge* (**14**:446) places this type among the Chytridiales, but neither author appears to recognize the fact that it has any relationship to the Enterobryae, to which it undoubtedly belongs. The only character which might separate it from the type genus *Enterobryus* is found in the presence of definitely differentiated spores, which replace, or succeed, the terminally abjointed segments which are characteristic of all the species of this genus; but whether this character should be regarded as separating the two types generically, or as extending our knowledge of the little known life cycle of the last mentioned genus, it is not at present possible to decide. In the numerous forms of *Enterobryus* which I have examined, none that have been observed growing within the intestine of the host have shown a development of well differentiated spores; although the terminally abjointed segments may be more or less sporelike, according as they are longer or shorter. It does not seem possible, however, to homologize them closely with the spores of the form described by HAUPTFLEISCH, or with those of the new form described later. It is nevertheless quite possible that, as in many cases among the

higher fungi, certain species of the same genus may be sporiferous in a special way, while others are not; or that differences in environment may bring about the sporulation of species which normally reproduce by separated segments only. In the two instances under consideration, for example, the individuals do not, like most species of *Enterobryus*, grow submerged in the more or less fluid contents of the ventriculus, or smaller intestine, in which the food ingested by the host has only partially been digested; and while the species of HAUPTFLEISCH is attached just within the anus, the new form is found growing on the hard external chitinous plates about the opening. As far as the possible food relations of these two forms is concerned, the situation seems to be quite different, since they come in contact with fecal matters only, which might be supposed to exercise a definite influence on their course of development. It should be mentioned, however, that although I have, in one instance at least, obtained abundant material of what appear to be several species of *Enterobryus* growing outside the anus of a *Passalus* from Grenada, B.W.I., none of the individuals, although they are otherwise very similar, show the sporulation which is so conspicuous a feature in the new form to be described.

This form is characterized by the possession of a huge basal cell; its very thick wall often laminate above, filled with a coarsely granular protoplasm, and attached at its base by a well developed sucker-like attachment entirely similar to that of other species of *Enterobryus*. The primary axis is at first continuous (fig. 47*a*), but later a terminal segment of considerable length is separated, and at least one more may be similarly formed, as in fig. 47*b*, in which a terminal scar shows very clearly that a segment of this sort has previously been abjointed. Such a condition, were it found within the intestine, would inevitably be regarded as belonging to some species of the genus *Enterobryus*. After one or more of these segments has been abjointed, and as a result of the activity of the denser multinucleate protoplasm at the end of the cell below the scar (fig. 51), a series of flattened cells begins to be cut off, each of which is supplied with a single large nucleus. Soon after these cells, or spore-segments, have been separated, they become ab-

ruptly compressed, so that above the fourth or fifth cell, as a rule, the series, when viewed edgewise, is thin and flattened, as is shown in fig. 47. The cells appear to be spore mother cells, within which thin-walled, sausage-shaped spores are firmly held by the thickened sheath which surrounds them and is continuous with the wall of the basal cell from which they were originally separated. As far as can be determined from the material available, these spores, which become eventually multinucleate, are separated by the breaking off of the whole or a portion of the series, and are not set free individually, as seems to be the case in the thin-walled species described by HAUPTFLEISCH. What the further history of their development is cannot definitely be stated. It seems probable that the spore groups are ingested by the xylophagous host, together with other spores of fungi which are present on their natural food, and that, separating as a result of the action of digestive fluids, they either pass through a preliminary period of growth attached to the wall of the digestive tract, or, in being voided with the excrement, become attached and develop at the mouth of the anus.

Although this species differs in its very thick walls, and in the form and more or less permanent association of its spores in series, its characters seem to correspond in all essential respects with those which are said to distinguish *Astreptonema*. Fig. 10 of HAUPTFLEISCH'S plate would indicate that his species is characterized by the separation of one or more terminal segments, which precedes the formation of spores. That these may be antheridia, as he suggests, seems quite improbable, and since, as he states, his material was somewhat scanty, it may prove that in this respect as well as in others the two show a very close correspondence. The cytological characteristics seem to be identical. The nuclei in both are large and rather numerous in the primary cell, more so in the denser contents of the distal region, where the spore segments are cut off (fig. 51), there being fewer toward the base, although one seems to be almost always present just above the foot (fig. 49). This foot is entirely similar in both and identical with the corresponding organ of *Enterobryus;* and the spores, although differing in shape and method of association when mature, are produced in a

similar way within mother cells. There can be little doubt as to the generic identity of the two forms, yet their characters are so similar to those of *Enterobryus* that I have preferred to use this generic name, in view of the fact that in no instance has the complete history of a species of this genus been satisfactorily observed.

Enterobryus compressus, nov. sp.—Hyaline to pale dirty yellowish. Basal cell very large and thick-walled, somewhat broader distally, 500–850×28–35 μ, straight or usually slightly curved at the base, attached by a well defined, slightly brownish yellow foot, shaped like an inverted cup, and distinguished by a slight constriction from the basal cell, which bulges more strongly on one side above it. Segments separated from younger specimens about 200×18 μ, their formation followed by the production of spore mother cells which are formed at the distal end of the basal cell, the series above the fourth or fifth cell becoming broad and flat through compression; the cells about 8 μ long by 35 μ broad by 18 μ thick, each containing a single spore which nearly fills the cavity, surrounded by a thick sheath continuous with the wall of the basal cell.

Growing wholly exposed on the anal plates of a large species of *Passalus*, Dominica, B.W.I., no. 2170, M.C.Z.

The unusually thick walls of this species and the coherence of its spore mother cells no doubt are influenced by its aerial habit, as a result of which it may be exposed to very dry conditions. The individuals represented in fig. 47, with two exceptions, are very old, and seem from the broken outline of their distal ends to have already shed a portion of the spore mother cells. In a majority of the sporiferous individuals, however, it is possible to distinguish the scar clearly shown in figs. 50, 51, from which it may be assumed that a segment has been separated, such as is shown in fig. 47*b*. A large number of Enterobryae have also been obtained growing in the same position on a species of *Passalus* from Grenada, which seems to include more than one species, the larger of which resembles the present form in all respects, except for the absence of any sporulating individuals. All of these, although their walls are somewhat thicker than is normally the case, would be referred without hesitation to *Enterobryus*.

The nuclei shown in figs. 48 and 51 are readily observed in the alcoholic material by decolorizing, after staining with Haidenhain's iron alum haematoxylin. The conditions shown are entirely similar to those described by HAUPTFLEISCH, and serve to show that these plants cannot under any circumstances be related to the higher bacteria, as has been suggested. One may admit that

they must be placed among the Phycomycetes; but they appear to occupy a very isolated position, and it is difficult to agree with this author that they have any close relation to the Saprolegniaceae.

In regard to their relation to the host, it may be said that the aerial habit of the present form seems to exclude the theory that these plants are purely commensalists, since they can only come in contact with the voided feces; and this fact, taken in connection with their highly specialized sucker-like attachment, suggests that they may be, to some extent at least, truly parasitic.

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EXPLANATION OF PLATES I–V

The figures are reduced from camera drawings made with Zeiss dry objectives and eyepieces and Leitz water (no. 10) and oil (1/16) immersion as indicated.

Cantharosphaeria chilensis Thaxter

FIG. 1.—Portion of host greatly magnified, showing distribution of perithecia.

FIG. 2.—Mycelium associated with perithecia; 10, 4.

FIG. 3.—Three perithecia among spines on host; D, 2.

FIGS. 4–5.—Ascus and ascospores; 1/16, 18.

Termitaria coronata Thaxter

FIG. 6.—Young individual showing preliminary stage; subdiagrammatic; D, 4.

FIGS. 7–8.—General appearance of mature fungus growing on leg and thorax respectively; former showing blackened primary attachment which shows through hymenium in center; D, 4.

FIG. 9.—Habit of growth on host; ×25.

FIG. 10.—Section of mature sporodochium, showing hypertrophied cells of host below chitinous integument; dark line of primary thallus shown, succeeded by fundamental layer, and sporogenous region, showing two primary zones, in upper of which a further differentiation into two zones is indicated; sporodochium traversed by two hairs arising from integument of host; semidiagrammatic; D, 1.

FIG. 11.—Hymenium seen from above, showing distribution of toothlike projections from sporophores; 1/16, 12.

FIG. 12.—Sporophores with included spores; semidiagrammatic; 1/16, 12.

Termitaria Snyderi Thaxter

FIG. 13.—Portion of preliminary stage, showing margin and chlamydospores; 10, 4.

FIG. 14.—Portion of section of old individual, showing hypertrophied cells of host below slightly intruded primary attachment, blackened primary

layer, with a few chlamydospores *in situ*, fundamental layer, and above it sporogenous region, comprising two zones, lower distally blackened; 10, 4.

FIG. 15.—Sporophores seen end on, showing terminal perforation; 1/16, 12.

FIG. 16.—Sporophores seen in section, showing origin from cells of fundamental layer, spore, and terminal perforation; 1/16, 12.

FIG. 17.—Free spores; 1/16, 12.

Muiogone Medusae Thaxter

FIG. 18.—Young spore developing from proliferous end of old sporophore; 10, 4.

FIG. 19.—Later stage of young spore of third order resulting from proliferation of second order; 10, 4.

FIGS. 20–21.—Older primary spores; 10, 4.

FIG. 22.—Spore showing origin of terminal appendages; 10, 4.

FIG. 23.—Mature spores, appendages bearing a few secondary spores; 10, 4.

FIG. 24.—Portion of appendage with secondary spores; 10, 18.

FIG. 25.—Group of spores in different stages of development.

Muiaria curvata Thaxter

FIG. 26.—Single plant bearing two mature spores drawn in outline; D, 4.

FIG. 27.—Single spore seen in surface view; D, 4.

Muiaria fasciculata Thaxter

FIG. 28.—Single spore seen in surface view; D, 4.

FIG. 29.—Single plant with several spores in different stages of development and numerous sterile filaments; D, 4.

Aposporella gracilis Thaxter

FIG. 30.—Two plants on wing of fly; D, 4.

FIG. 31.—Two branches, one unbroken, other proliferous.

Coreomycetopsis oedipus Thaxter

FIG. 32.—Young individual of unmodified superposed cells; 10, 4.

FIG. 33.—Young individual, division beginning in an intercalary cell; 10, 4.

FIG. 34.—Mature individual in which septa above intercalary cell have disappeared, forming continuous cavity within which spores are being abjointed; 10, 4.

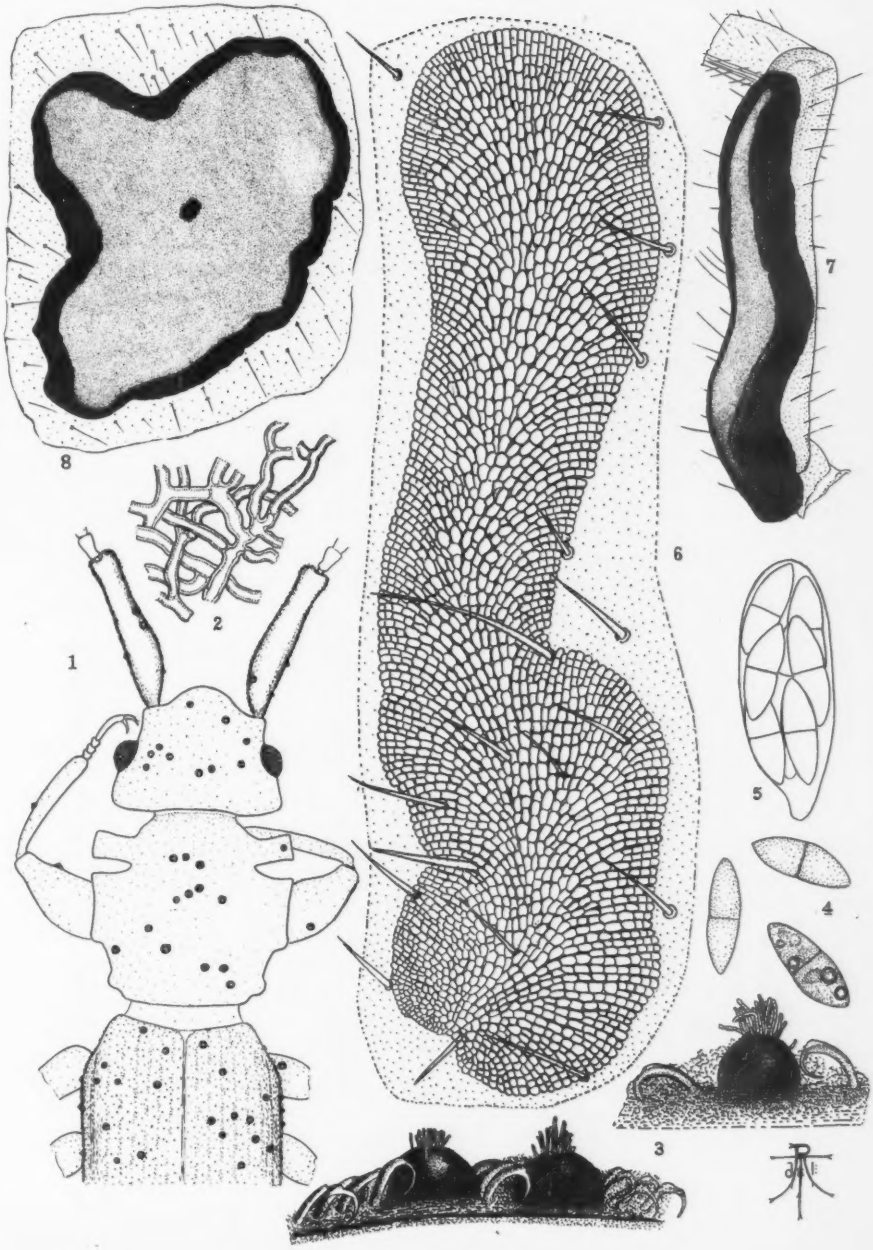
FIG. 35.—Younger individual in which terminal cells are beginning to disorganize, 4 septa still remaining above sporogenous hyphae; 10, 4.

FIG. 36.—Spores separated by crushing; 10, 12.

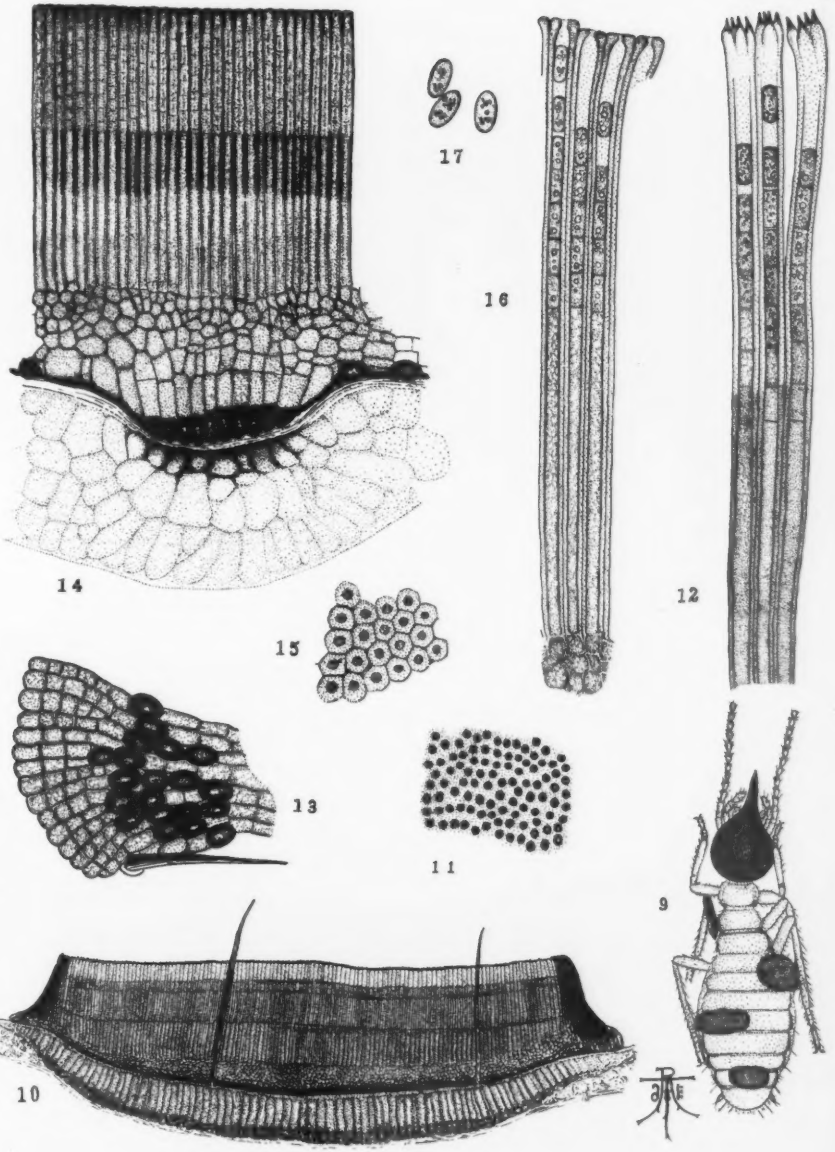
Thaxteriola nigromarginata Thaxter

FIG. 37.—Mature individual; 10, 4.

FIG. 38.—Two individuals *in situ* on spine of host, left one turned to show partly posterior view; 10, 4.



THAXTER on FUNGUS-PARASITES



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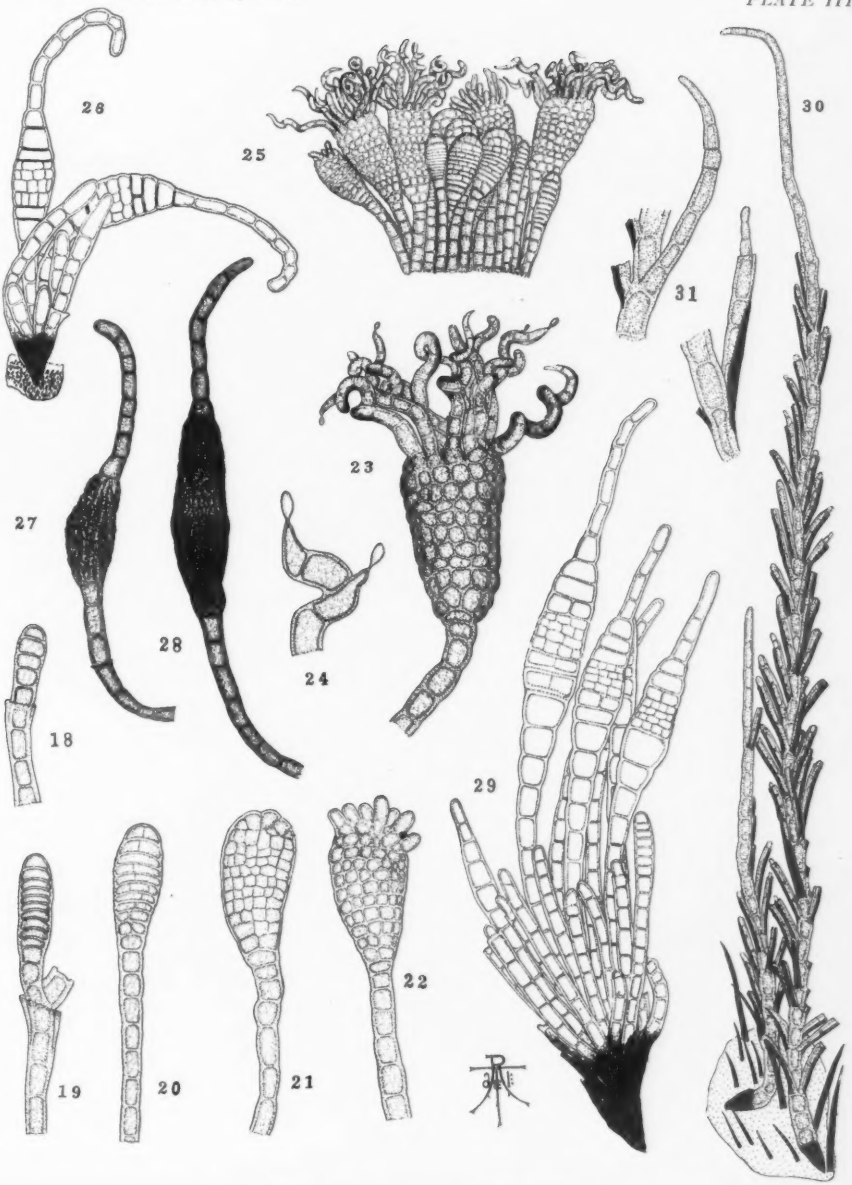

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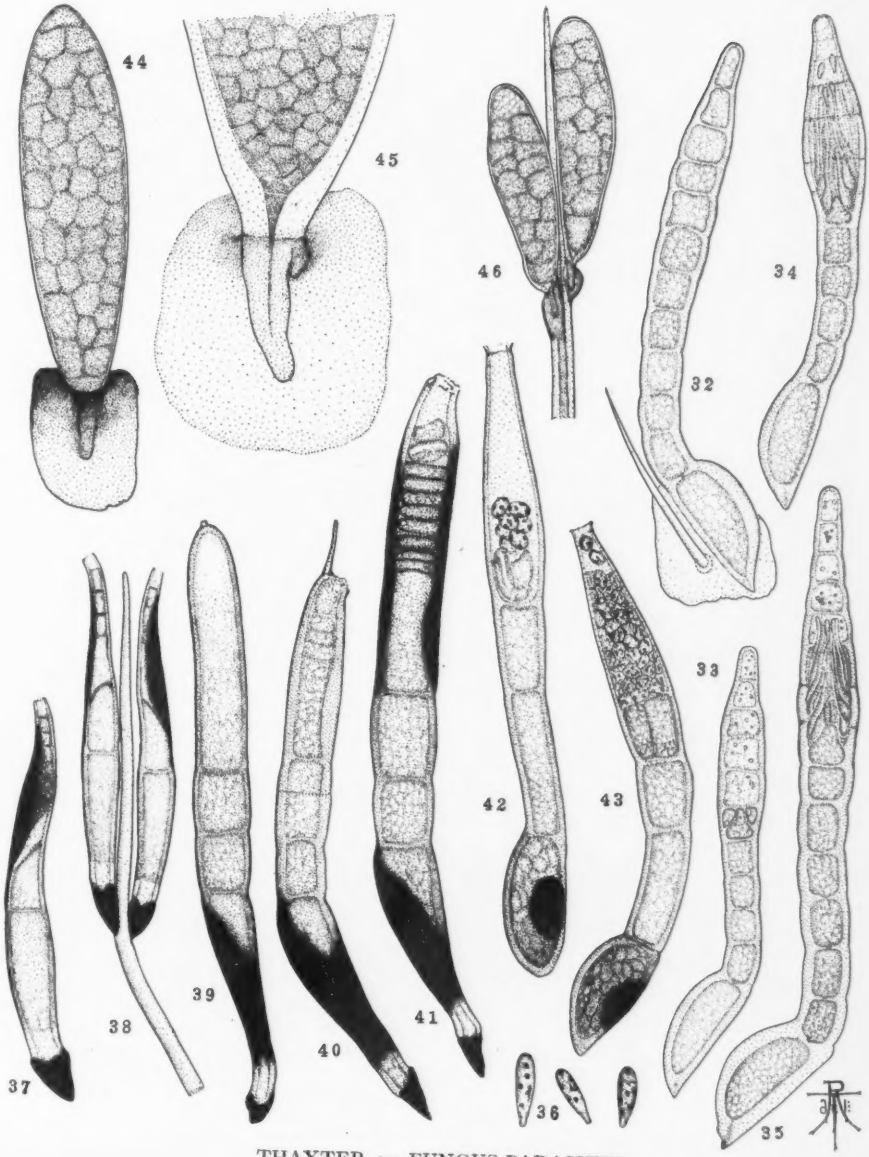

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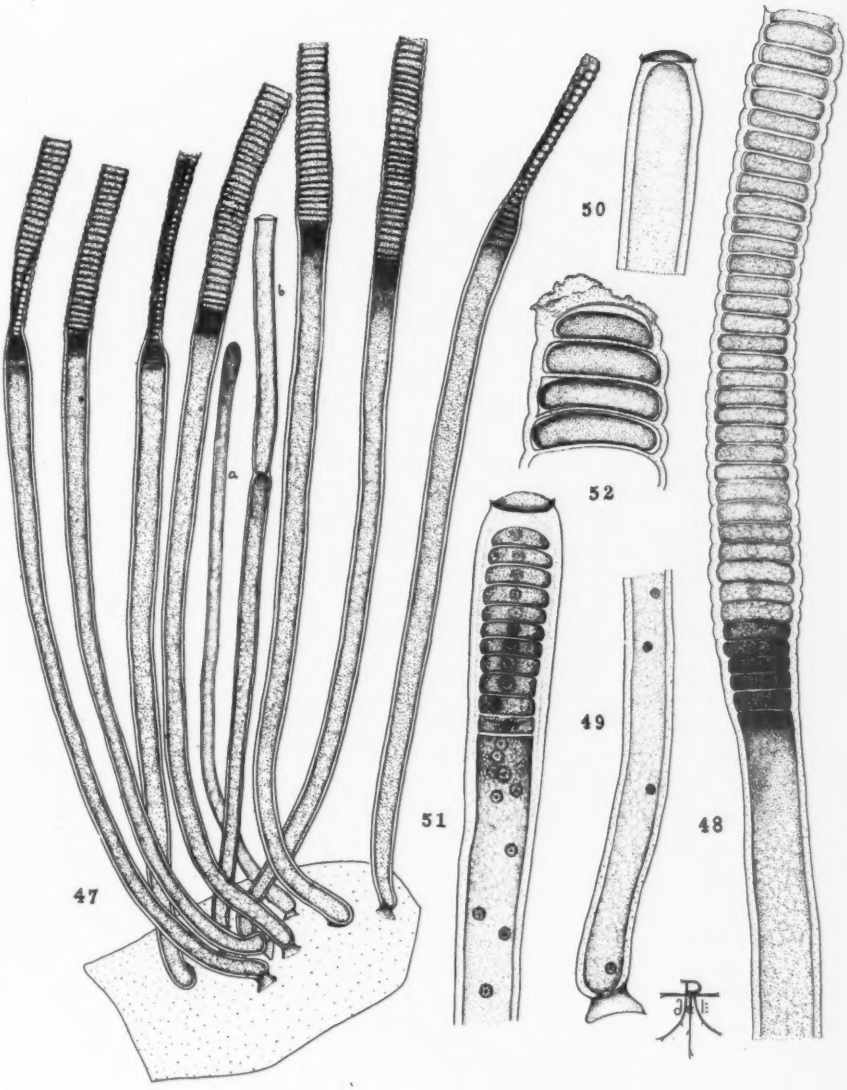

THAXTER on FUNGUS-PARASITES

Endosporella Diopsidis Thaxter

FIG. 39.—Young individual in which sporulation has not begun, although terminal spine has been broken off; 10, 4.

FIG. 40.—Older individual, spine persistent and sporulation beginning; 10, 4.

FIG. 41.—Mature individual, distally perforate; 10, 4.

Laboulbeniopsis Termitarius Thaxter

FIG. 42.—Mature individuals, basal cells of sporogonium disorganized, a few residual somewhat swollen spores remaining; 10, 4.

FIG. 43.—Mature individual, spores beginning to escape; 10, 4.

Amphoromorpha Blattina Thaxter

FIG. 44.—Front view of mature individual removed *in toto* from antenna of host, showing unevenly spreading secretion over simple rhizoidal foot; 10, 4.

Amphoromorpha entomophila Thaxter

FIG. 45.—Base of mature individual completely filled with spores and with no large basal cell, showing rhizoidal foot and secretion as in preceding figure; 10, 4.

Amphoromorpha sp.

FIG. 46.—Two individuals growing on antennal hair; foot seen laterally, but visible through transparent secretion; 10, 4.

UPLAND SOCIETIES OF PETOSKEY–WALLOON LAKE REGION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 256

H. D. CLAYBERG

(WITH ONE FIGURE)

Introduction

The writer became familiar with this region through spending the summers there for the past 12 years. During this time the rapid destruction of the few wild areas left suggested that studies be made while natural remnants were still available. The observations on which this paper is based have been carried on for at least three years. Besides the general data, 40 quadrats were made and a map of the plant geography (to be published later) was drawn.

The topography of this area was largely determined during the Pleistocene and Postglacial. LEVERETT and TAYLOR (**16, 17**) have covered this phase ably. At the time of the formation of Lake Chicago beaches this region was ice-bound, later forming part of the submersed area which gradually emerged as the waters changed from Lake Algonquin to the Nipissing Great Lakes, and through the Post-Nipissing stages to end in Lake Michigan. This periodic subsidence left the Algonquin, Nipissing, and later beaches (together with scattered morainal lakes inland), but erosion here has eaten away much of the Post-Nipissing levels.

The region at present is underlaid with Devonian deposits. Inland the surface layer is Upper Devonian, being largely black Antrim shale; while a marginal strip of about 3 km., from Petoskey west, and all territory north of the south margin of the Inland Route are covered with Middle Devonian. The latter contains the Petoskey limestone, which outcrops along the shore of Little Traverse Bay, either as shelving bedrock or limestone cliffs, the beds dipping inland. The lakes and channels have a layer of subaqueously deposited sand, covered in most places by black muck (fig. 1).

The region studied lies in Emmet and Charlevoix counties, Michigan. It includes a strip about 2 km. wide along Little Traverse Bay from Bay Shore to Idylwilde, together with Walloon

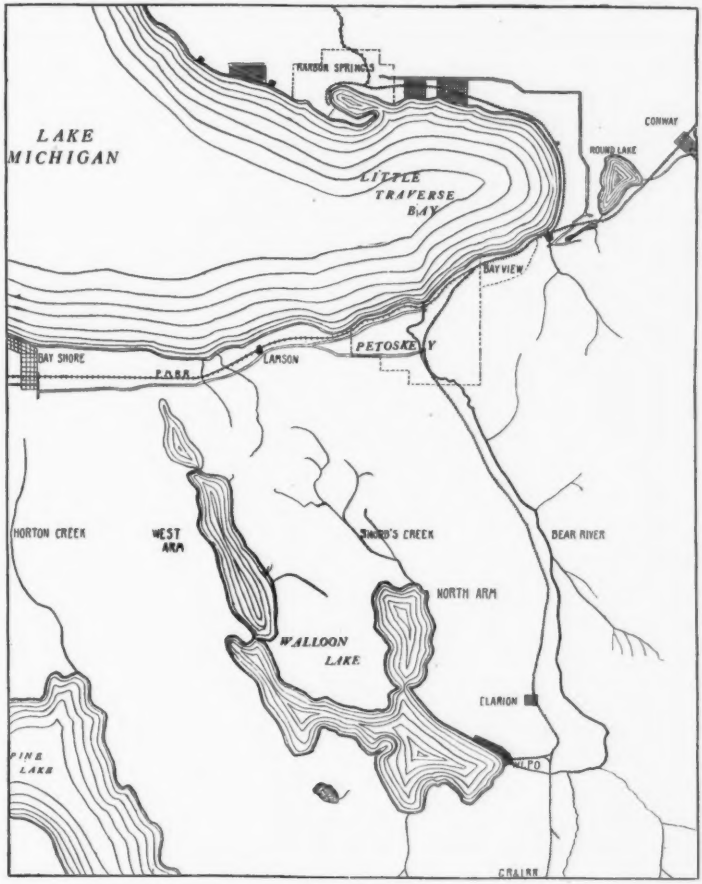

FIG. 1

Lake and surrounding shores. Bear Creek and Resort townships in Emmet County are also included.

The area of the region exceeds 260 sq. km. (about 100 sq. mi., of which about four remain in forest) and includes four upland

masses, one between Pine and Walloon lakes, another between Bear Valley and Walloon Lake, a third between the latter and the Inland Route, and a fourth north of the Inland Route. Inland Route is a valley extending from Kegomic to Cheboygan, with a continuous water channel running through it, beginning with Round Lake on Little Traverse Bay and emptying through Cheboygan River. While the only river of any size is Bear River (flowing through a broad and deep valley northward to Petoskey), many small creeks empty into the lakes and into Lake Michigan.

The topography is irregular and hilly, the upland being mostly highest behind the Algonquin bluff, sloping gradually down to the southeast in the territory south of the Inland Route, and to the northeast in the portion north of the same. The varied glaciated topography suggests wide floristic diversity, combined with youthful form (**6**), and this is the actual state found. The region was entirely covered with forest before settlement; the uplands with the climax maple-beech forest of the region, and the channels like the Bear Valley, together with the swamps and creek valleys, being mostly a continuous stand of *Thuja occidentalis* L.

The classification of COWLES (**5, 6**) has been found more suitable in analyzing the formations of the region, but this may partly be due to the fact that less soil diversity was observed than found by WHITFORD (**25**) along Lake Superior, so that an edaphic arrangement seemed less desirable. The edaphic factor, however, could not be excluded, as in cases where one type of soil alone was studied (**9**, p. 46). COONS divides his successions into swamp (lagoon→forest) and sand (beach→pine barren) series (**20**, p. 60).

Upland types preceding climax

The upland societies remaining include only the late tree stages, the earlier ones being lost. For convenience of treatment similar areas in the older parts of other series will be discussed here. Three apparent stages are seen.

PINE FOREST

Only *Pinus Strobus* L. and *P. resinosa* Ait. occur. *P. Banksiana* Lam. has not been found, although it occurs around the south end

of Lake Michigan, and in the pine barrens of northern Michigan as near as Wolverine in Cheboygan County. In general, the pine occurs in three places: (1) on the high hills back of Walloon Lake, (2) on Algonquin and Nipissing bluffs, and (3) as an early stage in dune forest succession.

The first location is a xerophytic open society of red pine sloping southward to the lake. The herbage below is dominated by ericads such as *Gaultheria procumbens* L. and *Vaccinium vacillans* Kalm. Occasional artificial clearings show an apparently succeeding stage whose components are crowded and mainly of shrub size. Here *Cornus* (*Baileyi ?*) and *Viburnum acerifolium* L. dominate. Following this is an obviously secondary society (may be absent in the primary series), taller than the preceding one and primarily *Betula alba* L. var. *papyrifera* Spach., with a mixture of *Populus grandidentata* Michx. and *P. tremuloides* Michx. Oak seems to follow.

The second type, almost entirely white pine, shows the oldest pines seen, growing on slopes approaching 45°, with sparse vegetation below characterized by *Solidago racemosa* Greene and *Shepherdia canadensis* Nutt. The xerophytic conditions here obtaining are indicated by leaves of *Aralia nudicaulis* L. 12 cm. across and 10 cm. tall, as well as by beds of *Polytrichum commune* L. Where cleared, the succeeding thickets are white birch with some *Prunus pennsylvanica* L. f. and *Amelanchier*.

The third type is a mixture of the two species, with white pine dominating, but with other conifers present. Among the particularly characteristic undershrubs occurring are *Corylus rostrata* Ait. and *Rosa acicularis* Lindl., while the herbage is largely of the ericoid type. At Menonaqua the full series is seen, but north of Harbor Springs erosion has eaten back into the pine society; the xerophytic conditions resulting permit persistence of much of the dune flora (telescoped succession).

As at present limited, pine occurs here near water in positions exposed to direct wind and of noticeably xerophytic nature. This agrees with its probable status as a relict tree formerly covering the upland. TRANSEAU (**24**) believes conifers reached their present distribution in the lower peninsula of Michigan by way of the lake shores.

Oak forest

Quercus rubra L. furnishes an unimportant and rare type. Stands are seen near Walloon Lake, and on the Algonquin bluff north of Harbor Springs, which extend inland in places for some distance. This tree occupies the same sort of habitat as the pine, and probably succeeds the latter in certain areas. Oak also covers Harbor Point, a low Post-Nipissing area. The discontinuous distribution shown suggests relatively recent seeding at Walloon Lake. Along the bluff north of Harbor Springs oak succeeds pine, when trees of the former are near and the pines are far enough apart (or have been cut or burned off). This occurs especially where the slope is not steep. Invasion of the adjacent upland by oak has occurred in one place (5). *Quercus velutina* is absent from this region (13).

Hemlock forest

The few stands of *Tsuga canadensis* Carr. left are confined to areas similar to those bearing pine, but of less xerophytic nature. It appears that any area bearing hemlock in this region is ecologically prepared for the climax forest, for, aside from the fact that hemlock is more or less common in the climax forest itself, and that hemlock stands normally bear some deciduous trees, the undergrowth and seedlings of an open hemlock forest are usually deciduous, and where the trees are cut off the young growth is largely maple and beech. The periodic reproduction of conifers may have a disadvantageous influence on their persistence. On the low hills bordering Walloon Lake a nearly pure stand is common, running from an average of 20 cm. diameter to a maximum of 80 cm. In such a primary society few herbs or seedlings are scattered over the brown needle layer. The characteristic plants are *Taxus canadensis* Marsh, *Lycopodium lucidulum* Michx., *L. clavatum* L., *Clintonia borealis* Raf., and *Mitchella repens* L. Where cut off, the sapling flora is almost exclusively deciduous, being about 60 per cent *Acer saccharum* Marsh, mixed with *Fagus grandifolia* Ehr., *Acer pennsylvanicum* L., and *A. spicatum* Lam.

Beyond Menonaqua the pines adjoin a hemlock beech society, which very likely will succeed them. This represents the richest

hemlock type seen, probably because farthest from the shore and most sheltered from the wind. The presence of many balsam and some oak seedlings, and the absence of sugar maple, make the next stage uncertain. Dense thickets of *Corylus rostrata* Ait. and much *Taxus* are characteristic. The hemlock on a Post-Nipissing level west of Harbor Springs is similar, but is mixed with *Abies balsamea* Mill. and *Thuja occidentalis* L. The Algonquin cliff west of Petoskey in several places bears large hemlock stumps of uniform (71–75 cm.) diameter, indicating that it was once largely occupied by a fine hemlock forest. The trees were cut sometime ago, for the secondary forest is nearly grown (average diameter 25 cm.), being beech, sugar maple, and *Betula lutea* Michx. f. A constant associate on open banks and cliffs is *Polytrichum commune* L., taking here as prominent a place as *Taxus canadensis* does in the level and denser part of the forest.

Climax forest

Seriation

The composition of the climax primary forest of the region has long been considered constant from the time the maple and beech reach dominance and respectable age. This is true floristically, but not ecologically or physiologically; for a climax formation is static in species, but dynamic as to individuals. Analysis of sufficient territory shows the forest to be more or less of a patchwork composed of trees in varying stages of development.

Cooper (4) found the climax forest he studied to be a "complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little or no young growth beneath, those of a single group being approximately even-aged. This mosaic or patchwork changes kaleidoscopically through long time spaces, but the forest as a whole remains the same, changes in various parts balancing each other." His studies were of a coniferous forest. The climax here is deciduous, so differences are to be expected. The forest floor is lighter and the next generation starts sooner in the case of the maple-beech forest. The patches observed in the climax forest of this region are too large to consider as the result of one tree fall. Further, they

would all have to approach the oblong or elongate form, whereas they are irregular where discernible, for the maple-beech forest is not to be considered as either patches of cleanly distinct even-aged trees, or as continuous forest with each generation even-aged throughout. It rather varies between these two ideals as limits.

Since the seriation is of individuals, the climax is not final, but recurrent, and during the development of each rough area or patch certain ages are to be recognized, each with fairly definite form, height, and spacing. At any one locality they follow each other in regular order, two or more commonly superposed, and adjacent areas independent of each other.

Definition of these ages is attempted approximately as follows:

	Age	Average diameter	Average spacing	Average height	No. per 100 sq.m.
Seedling.....	1	5 mm.	40 cm.	40 cm.	670
Sapling.....	2	2 cm.	65 cm.	4 m.	300
Young adult....	3	15 cm.	3 m.	10 m.	10
Adult.....	4	50 cm.	6 m.	30 m.	3
Old tree.....	5	65–85 cm.	8–20 m.	35–40 m.	1

ECOLOGICAL LIFE HISTORY.—The flowers and fruits of the climax forest are mostly inconspicuous. Undeveloped fertile seeds are always present, as is shown by the abundant germination in clearings. The latter also emphasizes light as a critical factor.

Since the forest determines the intensity, amount, and continuity of the light penetrating, the number of seedlings (age 1) and their distribution depend largely on the forest's age. Many seedlings die, but are easily replaced. They seem rare, but in reality often average 7 per sq. m., forming a scattered layer 20–60 cm. in height. The typical seedling form shows a slender, often branched, stem. The leaves are loosely corymbed or in one or two horizontal layers. The oval foliage outline results from free lateral growth (perhaps also spread to catch maximum of light). Apparently most of them remain nearly stationary for years. The taller ones appear distorted and dying, as if starved for light, which seems to decrease approaching the base of the sapling foliage.

Removal of the old trees above (15) permits freer elongation of the saplings. The seedling stratum becomes better lighted and watered, due to recession of foliage above and roots below. More

seedlings germinate to fill the gaps, and elongation results in the formation of a new sapling stand (age 2) as the trees above reach age 4. The sapling axis is long and straight, forks and side branches equaling the stem are rare, and the foliate part of the tree, although polygonal in cross-section, approaches a right cylinder. The lowest branches are dead twigs, the later ones are horizontal or angle up.

A fine close sapling stand is the culmination in percentage of volume occupied. As the size of a stand increases, the distances between its trees increase also, and it is believed that a law will here be found to control relation of diameter and spacing of trees. The sapling age shows maximum increase in size for given decrease in number per unit area, hence competition between trees of equal age is keenest here.

With removal of another generation the saplings elongate, but intensity of vertical growth decreases, for the relatively open spacing permits lateral growth and reapproach to the typical broad form shown by isolated trees in field and pasture. In passing from the second to the third age a transition in branch form is seen, from the filiform type of evanescent branch to the massive type of permanent branch characteristic of the adult. These originate far above the sapling tops and hence are developed later. Comparison of the young adult and sapling stages with regard to ratio of height to breadth suggests partial etiolation in the latter. All saplings with forked axes are eliminated, since no adults are seen with forks at sapling level. Naturally a biaxial shoot is at a disadvantage under active competition with those supporting but one.

With further thinning of population the adult stage (age 4) is reached. This is the true ecological climax. The maximum foliage display and culmination of vitality are seen here. A typical tree was studied, felled, and measured. There was no sign of lost branches or decay, all branches bearing a rich display of leaves in normal position. The trunk was clean, straight, and subcylindric, with the lowest branch 25.3 m. from the ground. The diameter basally was 53 cm. and the tree was 32.5 m. tall. The crown was oval, with 12 major branches. The duramen showed a central cavity 8 cm. wide at the base, with its cone point ending about 2 m. above

ground. Because of this cavity the age could only be estimated by proportion; the tree was approximately 250 years old (allowing for thicker early rings).

The senile or last stage (age 5) is scattered, because definite spacing is lost. Many primary limbs are gone, adventitious branches along the trunk and on otherwise dead limbs and stubs taking up the work. The heartwood is largely rotted. The sawed-off stump of one very old tree showed a cross-diameter of 120 cm., but only a margin of 15 cm. around the outside was wood, the rest being hollow. The base, at or near ground level, is often inhabited by a colony of big ants, and the breaking point is normally at this place. A certain degree of pliability is still retained in ages 4 and 5. The latter are apt to sway widely in a wind, some creaking loudly also under the strain; yet the tree may stay thus at the verge of fall for years.

Approach of death is equally indicated by the crown where symmetry is lost by branch fall. The top of an old tree is always ragged. These trees attain the maximum of height and diameter. They represent a wider range of age, dimensions, and form than any other of the life stages, partly because of their liberty of freer development than the younger trees below.

The beech follows the maple in general, but it is stockier, broader, and shorter, reaching each age much more quickly. Its terminal bud is weaker, and the tree apex is often injured by falling trees, lightning, and other destructive agents, so that the nutrients go to several branches near the top. As a result it is strikingly deliquescent and rarely develops a bole over 15 m. in height below the branches.

STRATIFICATION

MAXIMUM COMPLEXITY.—Investigators in the tropics have noted 5–7 strata in the rain forest (21). These were primarily due to the leafing out of the various tree species at different levels. It has been assumed that little or no stratification occurred in the climax maple-beech forest, the belief being partly based on the poverty of tree species (but two or three important) and the far lower degree of luxuriance as compared with the tropical rain forest.

Lower forest.....	Soil stratum: here lie roots, youngest farthest up.
	Leaf stratum: thin crisp continuous layer.
	Herbage stratum: includes seedlings also (age 1).
Middle forest....	Sapling trunks: first really open stratum; shrubs here.
	Death stratum: layer of dead twigs below sapling foliage.
	Sapling synfolium: sapling foliage layer.
Upper forest.....	Tree trunk stratum: ample light first reached.
	Upper synfolium: broken zone of adult tree foliage.

The strata of any one generation are best shown and fullest developed at the sapling age. They are not so well formed in the seedling and are breaking down in ages 3 to 5. Only major layers are listed. For this reason the seedling synfolium is not accorded separate rank (although thicker than leaf stratum).

SYNFOLIUM.—The synfolium is the layer formed by leaves of trees of the same age. It is the result of photosynthetic need in crowded sessile individuals. It must be dealt with not only as compound, with the unit the foliage leaf, but also as a mass. The placing together of all the synthetic tissue of a group of trees is of serious ecological importance. The leaf placing, together with the crowding of the trees, makes the vertical section of an individual show a nearly rectangular foliage mass. The synfolium governs its depth by means of the light relation. It also controls the amount and composition of the herbage below. In the general discussion here given, the synfolium of the sapling is taken as type.

While the synfolium continually and gradually ascends as the trees grow (no sudden jumps), the history of the foliage layer shows characteristic stages. Since the seedlings are scattered, their foliage layer is discontinuous horizontally. It is very close to earth level and is but 20–40 cm. vertically. As the sapling age approaches, the small foliage masses fuse into a continuous layer, having a much greater vertical section, and both upper boundaries parallel, horizontal, and nearly flat. This is the ecologic climax of the synfolium; here it reaches its greatest definition and density. Most of the growth is strictly limited to the top at this age, but later ages show the maple in its true light as more typically a deliquescent tree.

At the sapling age the synfoliar depth (from its top to its bottom) is 3–4 m. As it recedes from the ground its upper surface becomes

uneven and covered with the free cones of the young adults, while spaces creep up from below. These result because lateral growth is insufficient to maintain closure. Increased lateral spacing now permits increased lateral growth, one of the prime factors slowing vertical elongation. Approaching the adult stage (age 4) the layer breaks up into its component tree masses. This occurs by rifting (vertical or horizontal breaks due to tree or branch fall), the gaps becoming nearly unfillable at age 3, for closure is either by elongation of a younger tree or by lateral growth of the adjacent tree circle. This age is the first one free vertically and laterally.

A further step is the breaking up of a tree unit into foliage clumps, one or several to a branch. Finally, many of the oldest lose all primary foliage, the trunk and branches bearing scattered handfuls of leaves. This secondary foliage is borne on slender twigs developed from adventitious buds. Gradual fall of the last age destroys all semblance of a foliage stratum.

Recession occurs in two main ways (trunk elongation unimportant): by shedding of leaves and branches at the synfolium base (the synfolium is self-pruning during the growing season), and by apical growth, the stems adding new leaves and branches, thus extending the synfolium compass vertically. With increase of synfoliar distance (from ground) and rifting, the herbage layer receives increasingly stronger light; thus the tree seedlings are stimulated to more active growth and the illumination of the forest floor decreases again.

The sapling synfolium contrasts with the trunk strata above and below, in apparent space occupied, color, and opacity. The lighting of the trunk stratum above is much greater, and that of the dead branch layer much less, being composed of flat, thin, horizontal tissue plates. The synfolium seems to have the ideal structure and arrangement for maximum of surface, light absorption, synthetic efficiency, and carbon dioxide use, together with the minimum material, volume occupation, and transpiration. The apparent effect on the eye gives impressive display and exaggerated idea of solidly filled space. This effect is heightened on passing from the bright sunlight into the dense shade of the forest.

YAPP (**26**) makes some interesting observations on evaporation at different levels in an English marsh, and SHERFF (**22**) on an

American marsh, finding evaporation rate proportional to height above the soil. These suggest that data on the levels of the climax forest of this region would be significant. GATES (8) compares evaporation at the chamaephytic layer in different societies but not at different levels. He believes evaporation a result, not a cause, of succession.

ENVIRONMENT

Competition is affected by several influences: physical and chemical factors, parasites, and individuals of the same or an older generation. Scattered among the herbage are tree seedlings, many of them dead or dying. In fact the younger the group, the more die. No competition between seedlings occurs except as two are found within short radius of each other. The critical competition for them occurs with the older trees in the form of light interception (most important) from above and nutrient interception from below. Since the lifting of the light inhibition is very slow in terms of potential seedling growth, the plasticity of seedlings becomes a factor. Being so adaptable, one can fit itself to any rift by lateral growth; occasionally one with over 90 per cent of its leaves on a far side branch will be found. Maximum spatial crowding is reached in the sapling age, and consequently the most critical competition of the life cycle occurs here.

Approaching the climax of elimination, the first to go are those with too few leaves in the light. Among other causes this may be due to shortness, distortion, slow growth, or accentuated crowding. There are more weaklings and distorted trees at this age than at any other, and in their removal comes the critical stage in spacing evolution; for removal of the very old trees above results in intensified elongation and more rapid destruction, since the spacing interval is increased 20–100 times before the third life age is reached. In general, the sapling race is not only a struggle for life by vertical elongation, but it is one in which the time element is crucial.

Having reached the third age, the tree is nearly immune from lateral competition, the permanent stand being formed here. Future struggles are against rot, parasites, wind, and weather, both root and branch systems now being amply competent to maintain life processes. Since the tree's juniors must be limited to what it

cannot use, survival remains with the soundest and best developed. The final picking off in ages 3 to 5 seems slight. In the last age the result of unequal battle with parasites comes out and all fall in turn. It is the rare exception that remains to the last age, one of 100,000 seedlings that have lived and died within its present sphere of influence (GLEASON). In the last age beech is largely replaced by maple in most localities, so that a pure maple-hemlock stand is found in places.

Seasonal periodicity is shown, for example, in the synfolium, present only during summer and part of spring and fall. Each fall it joins the preceding synfolia in the dead leaf layer, thus proving how little actual solid was in it. Chromatic periodicity is more accentuated than in Illinois. The synfolium is yellowish green in spring, quickly turning to the darker green retained through the summer. In fall the birches turn yellow and many maples scarlet. Growth periodicity is shown in the alternating periods of relatively slow growth and active elongation (especially of saplings), according as the inhibition of an older generation persists or is removed.

Evidences of dying or death are unobtrusive but ever present. Nature seems very wasteful in her development of adult trees. The number of saplings pinned down by débris is remarkable. Many are thus actively destroyed instead of passively dying for lack of light. It is needless death and destruction that should in large measure be eliminated by scientific forestry, thus obviating the waste of space and light taken to develop useless plants at the expense of those later useful. Below the sapling synfolium is a death layer which bears, aside from the trunks present, many dead and dying branches.

Branches do damage in proportion to their size, the culmination of destruction coming in the fall of an adult tree. Tree or branch fall is primarily caused by basal rotting. Wind, rain, or lightning is usually required to crack the last resistant marginal alburnum of a branch or unbalance the tree (which has a different type of balance from a branch, so that it can break through proportionally much more wood). The big tree rarely catches on others to remain propped for a while. It usually falls without warning, snatching off branches from its neighbors, and pinning down or lacerating

hundreds of young trees and saplings. There is thus left a natural glade to be closed by regenerative succession.

Competition and parasitism are the main causes of death. Destruction of branches at the synfolium base by lack of light is due partly to slower growth, but primarily to disadvantageous position. In old trees the most serious causes of death are boring insects, fungus rot, loss of foliage and branches, and (possibly) decreased vascular efficiency.

The parasites present are mainly insects and fungi. Neither show prominently in the forest, remaining more or less hidden except for fungus sporophores and many adult insects. Forest floor pileate forms are characteristically present, but individually not very abundant. COONS (**20**) points out that fungi may also be grouped in formations, certain species being characteristic of each type of habitat. Conditions in the climax forest, especially of the lower levels, favor fungus growth by the relative twilight, more equable temperature, and higher humidity prevailing.

Tunneling bark beetles are present, and, because *Tilia americana* L. and *Fraxinus nigra* Marsh. seem more often attacked, the insects may aid in keeping maple and beech dominant. These beetles, being cambium eaters, would seem more destructive than the duramen eaters, such as *Tremex columba* of maple and beech.

Leaf parasites (**23**) seem rather few. *Rhytisma acerinum* forms black blotches on maple and oak leaves. A similar fungus causes scarlet patches. Mites causing bag formation on the upper surface of maple leaves, and plant lice occur persistently; woolly aphids (*Schizoneura*) blight the alder, but rarely injure the hardwoods; several sorts of leaf-eating *Microlepidoptera* are found that are worst on the birches, while the tent caterpillars (*Clisiocampa*) confine their attention almost exclusively to rosaceous trees. Thus the maple and beech would seem to enjoy relative immunity from the more serious pests, which may aid in their retaining dominance. The débris includes leaves, twigs, branches, trunks, and stumps, most being found on the ground. Arrest is rare for very light objects (leaves and twigs) and for heavy large ones (trees), but for different reasons. The numbers of the different sorts of débris vary inversely with their size. The leaf layer at the ground surface,

furnishing protection and humus, is characteristic of the climax forest. Unlike conifer needles, the leaves fuse during the winter into a single tough layer averaging 2–5 mm. thick, thinnest in late summer and thickest in late fall. Its base continually decomposes, adding to the humus below.

Twigs are always abundant on the forest floor; and since the herbage is open they interfere little with it. Their fall is light and they reach the ground soon, being smooth and slender and not liable to catch. They are easily pushed aside by all plants. Branches often remain on the tree for some time after death, but combined action of basal rotting and weather eventually tears them loose. Yet even then one may not fall, at times hanging by a strand of cortex and alburnum that is often remarkably small, or it may catch on the parent or a nearby tree at one of the crotches or lower branches. Usually one large branch is found on every 3–10 sq. m. Annual vegetation can be hurt for but one season, but perennial aerial parts are injured permanently.

The fallen trunk rots slowly, leaving a soil ridge and a narrow lane for many years. Stumps rot as slowly into a low mound, but hemlocks remain standing as giant stubs 10–20 m. tall with the branches lost. Their wood rots until it cuts like putty, but the bark will hold up for many years, being thick and tough, rich in tannin, and not rotted by fungi or eaten by insects. Maples and beeches rarely leave such stubs, except as the result of fungus entrance some distance up the trunk. Those that are left do not stand long.

Lichens are found sparingly on trunks above the sapling synfolium and on exposed trees. They are also seen on the larger branches and are more common on the maples and hemlocks, because the beech affords poor foothold. A year after a big tree falls, however, its bark is covered by a luxuriant and varied growth of foliose lichens, in consonance with the removal of the substratum from a xerophytic to a richly mesophytic environment.

Mosses are not common on vertical trunks. Ferns are not seen as epiphytes in this region, though not from lack of either individuals or species. Both may be found growing on rotting stubs (not hemlock).

Floristics

Gates (7) and Coons (20) define many of the societies found in the region discussed here. It is hoped in a later paper to point out the differences observed from the floristic types recorded and described by these authors (1, 19).

Normal type.—This occupied practically all the uplands of the region before clearing. There are 70–90 per cent sugar maple, 5–30 per cent beech, and the hemlock is a constant tree also, running as high as 25 per cent in some localities. Since many of the forests are not strictly undisturbed and hemlock is taken first (for barking), a low percentage or absence of it may be thus explained in some instances. Other trees occur in varying but small proportions, among the more prominent being *Tilia americana* L., *Fraxinus nigra* Marsh, *Acer spicatum* Lam., *A. pennsylvanicum* L., *Ostrya virginiana* Koch, *Betula alba* L. var. *papyrifera* Spach, *Prunus pennsylvanica* L. f., *P. virginiana* L., *Betula lutea* Michx. f., *Acer rubrum* L., *Ulmus fulva* Michx., *U. americana* L., and *Staphylea trifolia* L.

As type of this forest a quadrat in the primary undisturbed forest back of Bay View was taken (500 sq. m. in 20 squares). There were 17 big trees here, averaging 47 cm. diameter, making the average area occupied 29 sq. m.; 8 of these being maple, 5 beech, and 4 hemlock, although the hemlock is more numerous than in much of the nearby woods. Below these trees was a fairly open stand of saplings, those over a meter in height numbering 649; of which 57.3 per cent were sugar maple, 30.1 per cent *Acer spicatum*, 6 per cent beech, the other trees present being *Acer pennsylvanicum*, *A. rubrum*, *Ulmus fulva*, and *Fraxinus nigra*. Their average diameter was found to be 1.41 cm.; the average number per square (25 sq. m.) was 32.5. In a square studied near Walloon Lake the number of saplings was 89 and the average diameter 1.9 cm. The larger size and number in the latter square were probably because it had no adult trees in or very near it, while the Bay View quadrat had, so that its saplings had received only part of the light and nutrients that would otherwise be available.

It will be noticed that *Acer pennsylvanicum* and *A. spicatum* are prominent at age 2 in the first quadrat, and also in some of the climax forest. This is a similar phenomenon, but more accentuated

than the one observed by COOPER (4) in regard to the balsam on Isle Royale. These two maples are ecologically of the sapling type; that is, they reach their highest development in a form ecologically equal to the second life age of the sugar maple. Beyond maturity they have such a high death rate that, although often as abundant as sugar maple at the sapling age, they are rarely represented in the third age. GLEASON'S (11) significant tabulation shows *Acer pennsylvanicum* as the dominant tree after clearing. The contrary occurrence from that of the maple is observed in the case of the hemlock, very few seedlings of which are seen in the climax forest, although a fair number of the adults are constantly present; for, because of scattered occurrence of young trees, it is not probable that the species is dying out.

Shrubs are not common through the climax forest. *Cornus alternifolia* L. f. is often seen in the Bay View woods. The characteristic shrubs of the region include *Sambucus racemosa* L., *Ribes Cynosbati* L. (transitions to *R. gracile* Michx. seem to occur), *R. lacustre* Poir. (along Little Traverse Bay), *Lonicera* (*L. hirsuta* Eaton is occasional along Little Traverse Bay), *Taxus canadensis* Marsh, *Rubus Idaeus* L., *R. allegheniensis* Porter, and *Aralia racemosa* L. The last is really an herb, but it is so tall and large that it is ecologically a shrub and occupies the shrub stratum.

The herbage of the climax forest is varied and fairly abundant. The prevernal flora is sun-loving and close, forming continuous masses of foliage composed of few species and many individuals. In the upland woods the dominant species is *Dicentra canadensis* Walp., but in the woods along Little Traverse Bay *Dentaria diphylla* Michx. appears more prominent. Transition forms to the summer flora occur; for example, *Caulophyllum thalictroides* Michx. is prevernal in leafing and flowering, while in fruit it is strictly aestival. *Allium tricoccum* Ait. also has prevernal leaves which die down before the scape appears in early summer.

The summer herbage is more scattered and richer in species, its richness varying with the age of the youngest tree generation. It is shade tolerant, and characterized by about 50 species. Particularly characteristic among them are *Botrychium virginianum* Sw., *Aspidium spinulosum* Sw., *Trillium grandiflorum* Salisb., *Maianthe-*

mum canadense Desf., *Tiarella cordifolia* L., *Geranium Bicknelli* Britton, *Mitchella repens* L., and *Aralia nudicaulis* L. A typical (1 sq. m.) quadrat at Walloon Lake contained *Geranium* 10, *Viola canadensis* 10, *Allium* 9, *Osmorhiza Claytoni* 2, *Galium triflorum* 1, *Dentaria* 2, grass 2, *Botrychium* 1.

At Bay View the herbs and shrubs show something of a tendency to segregation into patches dominated by different types. Three quadrats of a square meter each taken here were: (1) *Tiarella* 92, *Streptopus roseus* 8, *Dentaria* 4; (2) *Taxus* 24, *Dentaria* 8; (3) *Allium* 116.

VARIANTS.—Both xerarch and hydrarch types can be distinguished. The xerarch occurs on high or hilly ground and is both drier and more open. Either hemlock or beech is prominent. The hydrarch type, shown well behind Bay View, is found in valleys and low ground, either occurring along streams or bearing standing water part of the year. The characteristic trees are linden and yellow birch. The herbage is closed and rich, as many as 40 species being found. *Marchantia*, *Equisetum scirpoides* Michx., orchids such as *Listera convallarioides* Torr., *Impatiens biflora* Walt., *Viola canadensis* L., *Glyceria nervata* Trin., *Polygala paucifolia* Willd., *Habenaria* spp., and *Lycopus* spp. are common; but the most typical character is the large number of ferns. Among the more prominent are *Adiantum pedatum* L., *Asplenium angustifolium* Michx., *A. acrostichoides* Sw., *A. Filix-femina* Bernh., *Phegopteris Dryopteris* Fee, *P. polypodioides* Fee, and *Aspidium spinulosum* Sw.

NATURAL CLEARINGS.—Natural glades and openings occur throughout the primary forest. The fall of a tree is followed in a month or so by a rank herbage growth (11), not the fireweed-composite type often following lumbering, but largely composed of naturally native forest path and clearing species. Among these, by the second or third year, spring up suckers and seedlings of maple and beech, mixed with certain clearing tree species, which shade out much of the herbage growth in four to six years. In the healing of the forest gap the clearing trees may be prominent at first, but they are gradually replaced by the maple and beech in course of time. Among the clearing trees are *Prunus pennsylvanica* L., *P. virginiana* L., *Tilia americana* L., *Ostrya virginiana* Koch,

Ulmus fulva Michx., *Fraxinus nigra* Marsh., and *Betula alba* L. var. *papyrifera* Spach. The herbage is of such species as *Aralia racemosa* L., *A. nudicaulis* L., *Dactylis glomerata* L., *Panicum* spp., *Ranunculus abortivus* L., *Solidago caesia* L., *S. canadensis* L., *Osmorhiza Claytoni* Clarke, and *Geranium Bicknelli* Britton. *Rubus idaeus* L. often plays a large part if the clearing is not too small and the seeds are introduced at a time when room is available.

Secondary scrub and interference

Terminology suggested (3, pp. 145–166)

1. Revegetation
   a) Primary: original or primary vegetation of the area.
   b) Secondary: vegetation coming up after removal of primary society.
      (1) Repetitive: secondary succession following course of primary.
      (2) Nonrepetitive: not following primary.
2. Degree of interference
   a) Partial: few adult trees felled.
   b) Incomplete: all adult trees felled.
   c) Complete: all but herbage removed.
   d) Destructive: all vegetation removed; includes areas where refuse is burned off.
3. Recurrence of interference
   a) Simple: occurs once; area left alone thereafter.
   b) Repeated: interim for partial recovery allowed.
   c) Continuous: repeated at short intervals so that no recovery is allowed.
4. Terrain: left clean, dirty (refuse left), or burned
5. Successional phases
   a) Regressive: reversion to an earlier stage, or "lower" floristic type.
   b) Delayed: same stage but individuals of an earlier age.
   c) Static: approximately same stage and life age.
   d) Progressive: succession hastened.
6. Ecological state
   a) Stage: as used for some point in succession of species.
   b) Age: as used for some point in succession of individuals.

Xerarch treeless societies

The upland herb and shrub floras appear to show five secondary societies.

Fireweed society.—Most of its species are not native. In clearings, particularly those resulting from destructive interference, with dirty or burned terrain, strongly regressive changes occur,

especially where the soil is stirred up or the humus destroyed. It has been said (3, 9, 10) that this new association is not "lower" than a forest, since it is new, but regression can be conceived as meaning return to a stage where less use is made of the space and light available. Furthermore, forest will finally replace such a society, just as it blots out any naturally formed clearing. The change here is toward a physically and physiographically youthful aspect (rejuvenation of COWLES, 6). The surface soil gives the prevailing tone to the society, being gray or yellow, powdery, and nearly free of available water, radiating intense heat on a warm day.

Into this xerophytic habitat comes a clearing flora showing but a limited number of species, among which *Epilobium angustifolium* L. is dominant. Other species of importance are *Sisymbrium altissimum* L., *Erigeron canadensis* L., *Cirsium arvense* Scop., and *Verbascum Thapsus* L. Besides these occur also *Sisymbrium canescens* Nutt., *Lactuca scariola* L., *L. canadensis* L., *L. spicata* Hitch., *Ambrosia artemisiifolia* L., *Gnaphalium polycephalum* Michx., *Erechtites hieracifolia* Raf., *Sonchus asper* Hill., *S. arvensis* L., *Erigeron annuus* Pers., and *E. ramosus* BSP.

Most of these species have a profusion of wind-borne seeds, and they take possession by having seeds there, by resistance to harsh conditions, by rapid growth, and by seeding profusely over the area when once started, thus getting ahead of competitors. They are finally shaded out by saplings. Certain species of *Lactuca* were observed 3–4 m. tall, and while in "young" dry areas a society as scattered as in a desert may be found, in full development this flora can form a positively impenetrable jungle, particularly on hilly ground with a dirty terrain. Few societies in this region can show such a wide variation of form corresponding with as wide a range of environmental conditions.

THORN SOCIETY.—Its species are natives of the region. This society occurs much in natural clearings, but because artificial clearings and cutovers are so much more numerous in this region at present, the thorn flora is found mostly in such places. It is dominated first by *Rubus idaeus* L., which is commonly succeeded in turn by *R. allegheniensis* Porter. The latter can hold a patch for years against saplings when pickers are numerous enough to

keep the trees down; but if the patch be undisturbed, the sapling growth can replace blackberry in a few years (pin cherry in 3 or 4 years). The thorn species are widely sown by animals that eat the fruits, so their armament serves rather for climbing and individual protection than for keeping out animals. *Erigeron canadensis* L. is the commonest holdover from the fireweed flora. Forerunner saplings are also very usually present. Thus this stage serves as transition where herb and tree meet. It can hold a vicinity far longer than the fireweed society.

FERN SOCIETY.—*Pteris aquilina* L. occurs with some grass on xerarch areas. Because of its flat-topped habit and proneness to form a pure stand of fronds of equal age and height, this fern forms a synfolium at from 40–80 cm. from the ground, the distance varying with age. Bracken is commonly associated with grass sod, coming in after continuous destructive interference in the drier hilly upland and exposed shore hills. Aspen often is found with it, both entering particularly after fire (12). *Myrica asplenifolia* societies of farther south (Little Manistee to Brethren) appear to be equivalent.

MILKWEED SOCIETY.—The species is not native of the region. *Asclepias syriaca* L., while common as a weed, and found in all sorts of societies, also forms a persistent, ubiquitous, and actively invading society of its own on drier upland and lowland areas. Like *Pteris*, it is often associated with grass turf, possibly because of the natural openness of the two societies. It probably enters after more severe and continuous interference than the bracken can endure. Because of its underground rhizome, xerophytic structure, tremendous reproduction, and efficient seed dispersal, it can maintain itself after continued cutting and even plowing. It probably would precede sumac in reclamation of unused upland pastures, and is prominent where interference (and turf?) prevents later successional stages in pasture and grassy upland.

SUMAC SOCIETY.—These species are probably native here. *Rhus typhina* L. and *R. glabra* L. occur in upland pastures, along roads, and in clearings, being primarily a bordering association (thus later than milkweed), occurring more often on closed (and especially clay) soil. It forms a stand 1–2 m. high, much opener than the milkweed, and being taller permits more herbage. Along roads it is often

followed by maple-beech, although the regenerating climax forest can enter at any stage of the upland secondary series. One of the evidences suggesting equivalency of the thorn, fern, and milkweed societies is that sumac can follow any one, and that any of the three can succeed the fireweed flora.

Xerarch tree society

The aspen–white birch–pin cherry society varies much in general form and specific content, so three types (consocies) are found. The dominant trees are *Populus tremuloides* Michx., *P. grandidentata* Michx., *Betula alba papyrifera*, and *Prunus pennsylvanica* L.

Pin cherry–birch.—The birch may be absent. Pure pin cherry stands in particular occur in upland and middle level clearings following the thorn society. They can spring up suddenly. In spite of good light the lower branches remain slender and die early. The mode of growth is the arboreal expression of the clearing society type; all are also soft wooded. The pin cherry is ecologically peculiar in being strongly excurrent, with elongate form and filiform type of branches, wasting the minimum of tissue on laterals and trunk diameter. This gives it great power of vertical elongation, an aid in competition for place in clearings, but makes it short-lived; so in time it must give way to longer-lived hardwoods. Thus the forest of this type is fairly open, with good herbage.

Aspen–pin cherry.—This is a dry open xerarch type found along shore, especially on the ridge back of the Nipissing cliff. Often half the trees will be dead and the remainder equally divided between the two species. Herbage is scant or none, and dead twigs and branches are thick below. Such a stand is far opener than either maple-beech or cedar forest, although similar to the cedar in number of dead trees.

Aspen-Pteris.—This is found more on dry levels inland. The small-toothed aspen dominates (90 per cent or more); the large-toothed aspen is prominent; and some birch may be found. Being secondary, the herbage below the bracken synfolium suggests a high type of primary forest. The following species are found: *Gaultheria procumbens* L., *Cornus canadensis* L., *Lonicera hirsuta* Eat., *Corallorhiza* spp., and *Lycopodium tristachyum* Pursh. The

bracken seems to interfere little with this herbage, in fact may protect it. They occupy a different level and seem complementary (**22**).

The preceding types are alternative. Which enters depends on soil conditions, topography, and seeds present. Aspen succeeds best after fire and in higher dry ground. Pin cherry seeds are bird-scattered (and fertile longer), thus being more apt to reach a favorable place. The xerarch tree society is able to enter in many cases where climax forest is sufficiently cleared, either with or without intervention of treeless stages. The greater the degree and the quicker the recurrence of interference, the more likely regressive changes are to occur, its amount and the environment determining whether the ensuing secondary state be repetitive or non-repetitive, and, if the latter, whether it be thrown back to tree, shrub, or herb stage (the farthest being the fireweed semi-desert), that is, the degree of rejuvenation.

Regeneration of the climax forest may be speedy, hardwood saplings following a mixture of fireweed and thorn. This results in a remarkable floristic mixture. Behind Bay View a nearly pure stand of red maple has been formed after cut over. At Walloon Lake the beech is apt to dominate in the regenerating climax forest. In other places *Acer spicatum* and *A. pennsylvanicum* are important. If the xerarch tree society takes charge of a district it may be followed by yellow birch and elm (**18**) before the climax supervenes. Grass turf may prevent tree entrance (**11, 12**), but it would appear that milkweed and sumac, at least for dry upland, could replace it.

Discussion

The upland societies here studied show that most of the area of this character was occupied before settlement by climax forest. The forest itself (as any climax) is static in species but dynamic as to individuals, so that the climax is not final but recurrent. Five life ages may be singled out in this forest, each with its own dimensions and ecological characters. Thus the sapling age shows maximum increase in size for given decrease in number per unit area, so that competition between trees of equal age is keenest here.

For the foliage layer is coined the name synfolium, and its development and ecological significance are analyzed. In connection with mortality, it is pointed out that very many saplings are pinned down by débris, and thus actively destroyed instead of passively dying.

The study of Kent County, Michigan, by LIVINGSTON (18) shows five societies, while the writer has distinguished four here. While this might be interpreted as meaning Kent County was not so far advanced, it must be remembered that: (1) oak and hickory play more important rôles in succession in the Grand Rapids area than at the north end of the southern peninsula; (2) LIVINGSTON recognizes three societies containing oak, and two with maple; in this region the four primary types tend to be mutually exclusive; (3) LIVINGSTON uses herbs as well as trees in definition of his societies, which the author has not felt justified in doing for this region as yet.

In examining the distribution of the secondary societies, it seems probable that the hypothesis laid down by LIVINGSTON holds in large measure, but it may be that this is only for societies enduring rather small differences in moisture retaining power of the soil; for the fireweed society (secondary) is able to endure a wide range in this particular, being shaded out, but not dried or drowned out.

Throughout this region the response of the plant societies to interference and changed environment has been adaptive, in so far as their constitution allowed. Some natural societies, such as the blackberry, are fitted to survive in partly wild areas. Others can invade the fields in competition with the crops. Characters required are quick entry, speed of vertical growth, quickness of fruiting after germination, quantity of seed production, and efficiency of distribution; for a given society may be here today and gone tomorrow, plowed under.

The best example of the weed type among the societies previously discussed is the fireweed society, which contains species that are being rigidly selected by man in his fight against them. These plants are likely to survive long after the maple-beech society is banished to the wood lot and city parkway; for evolution is toward

the herbaceous annual type (as pointed out by SINNOTT and BAILEY in past evolution also), as best suited to the mobile environment furnished.

The author desires to extend his thanks to Professor HENRY C. COWLES, of the University of Chicago, whose help and encouragement have made the completion of this work possible. He also wishes to thank Mr. CHARLES W. FALLASS, of Petoskey, and Professor CHARLES H. SWIFT, of the University of Chicago, for their cooperation during the progress of the work.

OAK PARK, ILL.

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FIELD AND LABORATORY STUDIES OF VERBENA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 257

M. KANDA

(WITH PLATES VI–IX AND TWENTY-SIX FIGURES)

Introduction

In GRAY'S *New Manual of Botany* (edition of 1908), 8 species of *Verbena* are described as occurring in the Eastern United States. These are classified into two sections, of which the first is further subdivided into three groups. Five of the 8 species grow wild in the vicinity of Chicago, namely, *Verbena urticaefolia* L. and *V. bracteosa* Michx., belonging to the first and third groups respectively, and *V. angustifolia* Michx., *V. hastata* L., and *V. stricta* Vent. to the second group. These three last named species occur abundantly at Stony Island, a southern suburb of Chicago, where the conditions of prairie, damp, and dry ground are met with successively as one proceeds from the north to the south end of the locality. Here the three forms grow in their characteristic ecological situations: *V. stricta* on the prairie, *V. hastata* in damp low places, and *V. angustifolia* on high dry ground. On examining the *Verbena* plants, one is rather surprised to find that there are many intermediate forms which can scarcely be assigned to any of the three species with certainty. The question arises, therefore, as to whether they are hybrids or mutants of the three species.

The present work was undertaken to determine whether or not there are any cytological differences in the fertilization phenomena and early stages of development between these forms. The results were rather negative as regards the genetic nature of the intermediate forms; that is, with slight exceptions, no significant differences were found between them. Many of the observations upon the embryonic development, however, are sufficiently interesting to merit description. These will therefore constitute the chief subject matter of the present paper, such facts and suggestions as I am able to present regarding the origin and nature of the intermediate forms being added at the close.

This work was carried on at the Hull Botanical Laboratory, University of Chicago, under Professor CHARLES J. CHAMBERLAIN, to whom I wish to express my sincere thanks for suggesting the problem, and my appreciation of his kind advice throughout the progress of the work. My acknowledgments are also due to Professor JOHN M. COULTER for his kindness in placing the conveniences of the laboratory at my disposal.

Taxonomic observations

Although one can easily recognize the specific characters of the original species, *V. angustifolia*, *V. stricta*, and *V. hastata*, it is impossible to arrange the forms intermediate between them in a linear series with regard to all of their contrasting characters. In other words, all of the characters do not vary in the same direction, so that if one distributes them among the original species with reference to one character, a different distribution would be required for some other character. Examples of the 3 species and the 6 intermediate forms which I was able to collect are given in figs. 1–9 (pl. VI). Figs. 1, 3, and 7 are *V. angustifolia*, *V. stricta*, and *V. hastata* respectively, and the others are the intermediates arranged between the 3 species in accordance with their degree of similarity to them, as nearly as this could be determined. I have attempted to represent diagrammatically the morphological relationship between the originals and the intermediates by the triangle shown in text fig. 10; the numbers on the triangle refer to the figures in plate VI. The three apices (1, 3, 7) indicate the three original species, and the points along the sides of the triangle show the probable position of the intermediate forms with reference to them. For example, 4 is believed to be nearer to 3 than to 7, and 5 is probably about midway between 3 and 7. The contrasting characters of all of the forms are given in detail in table I.

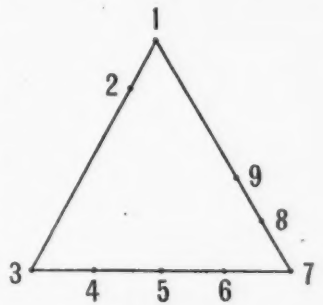


FIG. 10.—Diagrammatic representation of morphological relationship between originals and intermediates.

TABLE I

No.	Height in cm. in average	Stems			Leaves					Spikes		Corollas		Bracts
		Form of cross section	Branched or not	Stout (+) or slender (−)	Breadth in cm. in average	Length in cm. in average	Petiolated or sessile	Serrature double (+) or single (−)	Hair thick (+) or not (−)	Thick (+) or filiform (−)	Clustered (+) or loose (−)	Color	Size	Long (+) or short (−)
1...	25.2	Quadrangular	Apical part only	−	0.7	5.1	Sessile	−	− and rough	+ slightly	−	Pale purple	Medium	− and leafy
2...	30.0	Quadrangular	Apical part only	− but stronger than former	2.7	7.0	Sessile	−	+ and rough	+ than preceding	−	More violet than preceding	Slightly larger	+ and leafy
3...	88.0	Round	Not except sometimes at apical part	+	4.5	8.5	Sessile	+ heavy	+ and woolly	+ strongly	+	Purple	Large	+ and slightly leafy
4...	120.0	Round quadrangular	Not except sometimes at apical part	+	5.0	12.0	Short petioles	+ heavy	+ and slightly woolly	+	+	Purple	Large	−
5...	99.9	Round quadrangular	Not	+	3.2	9.0	Long petioles	+ slight	+ and rough	+	+ slightly	Lilac	Large	+ and narrow
6...	120.0	Quadrangular	Rare	+	2.7	8.5	Short petioles	+	+ rough and stiff	+ slightly	+ slightly	Purple	Slightly larger	−
7...	187.0	Quadrangular	Apical part only	+	2.5	11.4	Long petioles	+ slight	+ short	−	+	Purple lilac	Small	+ and narrow
8...	120.0	Quadrangular	Apical part only	Somewhat −	1.7	10.0	Long petioles	−	+ short	−	+ slightly	Pinkish purple	Slightly larger	−
9...	82.5	Quadrangular	Apical part only	Somewhat −	3.0	9.5	Long petioles	−	+ short	−	+	Pinkish purple	Slightly larger	−
1...	25.2	Quadrangular	Apical part only	−	0.7	5.1	Sessile	−	− and rough	+ slightly	−	Pale purple	Medium	− and leafy

It is necessary to consider whether or not the differences between these plants might not have been induced through adaptation and response to the local conditions in which each type may happen to be growing. Such an influence of local factors can be recognized at Stony Island in different degrees; thus, for instance, while the color of the flowers of *V. hastata* varies greatly with individuals, without reference to the conditions of the habitat, the shape and texture of the leaves of this species are plainly responsive to the surroundings, those plants growing in dry places having narrower and stiffer leaves than those inhabiting wet situations.

I believe I have eliminated this possibility in selecting my materials, and those which I regard as intermediate forms are not cases of modifications due to individual differences or adaptation to local conditions. Thus I have found forms 1 and 2 growing under the same external conditions at one location; forms 4, 5, and 6 growing together at another place; and forms 8 and 9 growing at a third spot.

Cytological observations

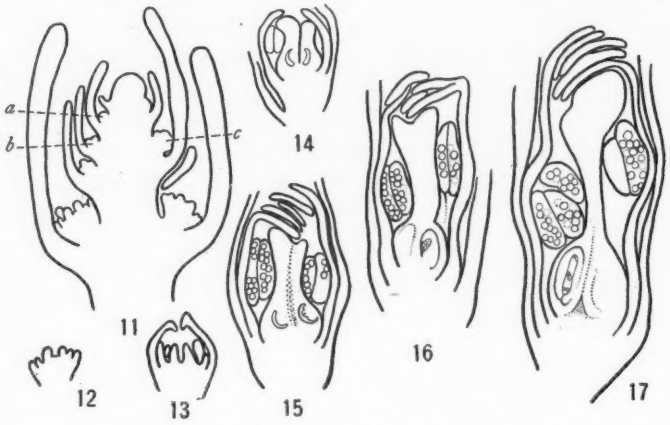
Material and methods

The spikes of *V. angustifolia* (fig. 1), *V. stricta* (fig. 3), and *V. hastata* (fig. 7), and the form intermediate between *stricta* and *hastata* (fig. 5) were collected during July and August 1918 at Stony Island. The apical part of the spikes, the pistils, and the young fruits in different stages of development were fixed in chrom-acetic acid and corrosive sublimate–acetic acid solutions, the former giving the best results. In the case of the pistils and fruits, it was found advantageous to pick off carefully or partially remove the calyx tubes, as they interfered with the rapid penetration of the fixing fluid. Sections of the apical part of the spikes were cut 5, 10, and 15 μ in thickness; pistils and young plants, 5 and 7.5 μ. Flemming's triple stain and iron alum haematoxylin were used, the former giving quite satisfactory results.

All of the four forms mentioned were examined in more or less complete series. *V. angustifolia* is chosen as a type for the purposes of description, but most of the statements are applicable to the others also, and they will be mentioned specifically only where differences between them make a separate discussion necessary.

DEVELOPMENT OF FLOWER

The first evidence of the formation of flowers is the appearance of papillae in the axils of the bracts (fig. 11*a*); these papillae are the primordia of the receptacles of the flowers. The outline of the receptacle soon becomes angular through the upward growth of four hemispherical protuberances from its distal surface (fig. 11*b*), and soon afterward its base produces a ring-shaped outgrowth (fig. 11*c*). The former develop into the stamens, and the ring immediately afterward separates into the corolla and the calyx



FIGS. 11–17.—Floral development in *V. angustifolia;* ×35

tube (fig. 12). The appearance of the carpels is indicated by a broadening of the receptacle (figs. 12, 13).

In fig. 13 the calyx tube has begun to curve inward over the top of the flower. Within this the corolla tube, the hemispherical young stamens and the two carpels appear in succession. Their later stages are shown in figs. 14–17.

DEVELOPMENT OF MEGASPORE AND EMBRYO SAC

When the ovule has reached the stage shown in fig. 15, the subepidermal megaspore mother cell that terminates the axial row of the nucellus can readily be distinguished from the surrounding cells through its larger size and large nucleus (fig. 18). The

megaspore mother cell and its nucleus with a prominent nucleolus continue to increase in size (fig. 19). Two divisions then occur which result in the typical formation of a row of four megaspores (figs. 20, 21); this takes place when the ovule is about at the stage represented in fig. 16. The innermost of the four megaspores is the largest, and is destined to develop into the embryo sac (fig. 22).

Successive stages in the development of this basal megaspore, accompanied by the destruction of the other three megaspores, are shown in figs. 22–25. The nucellus, consisting of a single layer of cells, surrounds the row of megaspores (fig. 21). It eventually becomes so distended by the enormous expansion of the developing embryo sac that it ruptures, and the ruptured nucellus is then carried downward as a cap on the growing embryo sac, as was previously described by MOTTIER (14) in *Arisaema*, CALDWELL (1) in *Lemna*, and MERRELL (13) in *Silphium*. In the next stage (fig. 26) the embryo sac lies free in the space between the funiculus and the integument, and the yellowish-brown remnants of the nucellus are observable capping the micropylar end of the sac.

27

FIG. 27.—*V. angustifolia:* mature pistil with mature embryo sac; ×35.

The phenomena of the enlargement of the sac, the division of its nuclei, and the destruction of the cells of the nucellus do not occur simultaneously, but these processes take place at different rates. The development of the megaspore and the fate of the nucellus are exactly the same as described by MERRELL for *Silphium*.

When the embryo sac reaches maturity (fig. 26), taken from an ovary in the stage represented in fig. 27, the sac is several times larger than it was when inclosed in the nucellus, very slender in shape, and always constricted just above the egg apparatus. The egg apparatus seems to be typical. The nucleus of the egg is several times larger than the nuclei of the synergids and contains

in the resting condition a fine chromatin network and a large, often vesicular, nucleolus. After the fusion of the polar nuclei, which occurs near the middle of the sac (fig. 25), the resulting endosperm nucleus approaches the egg apparatus. At this time, as shown in fig. 26, the endosperm nucleus still possesses two nucleoli, evidences of its binucleate origin, and is considerably larger than the egg nucleus. It is frequently in contact with the egg. There are three very small but typical antipodal cells.

The nutritive jacket surrounding the embryo sac of *Verbena* usually consists of a single layer of cells derived from the inner epidermal layer of the integument, and it develops especially at the micropylar end, investing the egg apparatus of the embryo sac. The cells of the jacket have conspicuous brownish contents, among which are numerous starch grains. Rather frequently a portion or portions of the jacket cells inclosing one or more grains of starch protrude into the embryo sac.

DEVELOPMENT OF MICROSPORES

At the stage shown in fig. 14 the hypodermal archesporial row is distinguishable, and the succeeding stages follow the usual course of development (figs. 28, 29). There may be only a single longitudinal row of spore mother cells, but one or two longitudinal divisions of the primary sporogenous row may take place (fig. 30).

The pollen mother cells within a loculus do not divide quite simultaneously, so that several different stages of the reduction division may be found among them (figs. 31–33). It is rather difficult to count the number of chromosomes in this species (*V. angustifolia*) because they are remarkably small and slender, but it was ascertained that 8 is the $2x$ number. In the second maturation division the two spindles usually lie across each other as in fig. 33.

In *V. angustifolia* there are two different types of tetrad formation. In the one case the peripheral cytoplasm of the pollen mother cell is left over to form a wall for the tetrad, this wall subsequently disintegrating (figs. 34, 35), while in the other case the entire mother cell is utilized in the formation of the tetrad (fig. 36). Figs. 37–41 give successive stages in the development of

the pollen grains. The wall of each microspore gradually thickens and sometimes a great many starch grains may be observed in the interior (fig. 39). Cases of accumulation of starch grains in the pollen have been reported by MURBECK (15), ISHIKAWA (11), and others. In *Oenothera* ISHIKAWA states that "the plasm containing starch grains in the pollen tube is poured into the attacked synergid," but in this case no starch is present in the pollen tube (fig. 42). A large vacuole appears in the pollen grain for a time (fig. 40), but it soon fades away and the first vegetative cell is cut off (fig. 41). More advanced stages could not be observed, as the contents and wall of the pollen grains become extremely dark in color. While these changes are occurring, the tapetum and middle layer disintegrate.

FERTILIZATION

It is very difficult to obtain clear pictures of the stages in which the male nuclei are on the point of fusing with the egg cell and the endosperm nucleus. In the first place the egg apparatus is rendered very indistinct through the presence of deeply staining cytoplasmic substances around it. I believe this deeply staining material is the result of a concentration of the cytoplasm and the inclusion within it of nutritive substances destined for the endosperm. The abundance especially of starch grains around the egg apparatus greatly confuses its appearance with the gentian violet stain. Secondly, the synergids seem to be more ephemeral in *Verbena* than in other plants, and soon become converted into a tenacious mucus-like material. This material from the disorganized synergids also stains very deeply. Thirdly, when the pollen tube enters the egg apparatus, a part of the disorganized nucellar cap penetrates into it with the tube and always gives rise to a figure of peculiar shape and staining properties (figs. 42–44, 46). MERRELL states that in *Silphium* "the pollen tube passes along the outside of the cap which usually crowns the embryo sac and enters the sac just beyond its free margin." In *Verbena*, however, the pollen tube, entering the sac at the micropylar end, thrusts itself through the nucellar cap (fig. 42), just as in *Lemna*, described by CALDWELL.

Figs. 43 and 44 show stages of fusion of the male and female nuclei. In fig. 43 one of the male nuclei is in contact with the egg and the other with the embryo sac nucleus, and in fig. 44 one of the male nuclei has fused with the egg nucleus.

In connection with the fertilization process it should be reported that at this time a proteid-like substance makes its appearance in the cavity between the carpels and ovules (figs. 26, 27). This material forms a network, probably as the result of coagulation by the fixing agent, and stains deeply with cytoplasmic dyes. The only suggestion which can be offered as to the function of this substance is that it may be related to the nutrition of the pollen tube, since it appears just before fertilization and disappears shortly after that process is completed.

Formation of endosperm

After fertilization the primary endosperm nucleus moves toward the center of the embryo sac, and its first division takes place there. This division is followed by the formation of a wall which divides the sac into two approximately equal chambers, the micropylar and the antipodal chambers (figs. 45, 46). Such a formation of a two-chambered embryo sac has been observed in many plants, both monocotyledons and dicotyledons, by Hofmeister (10), Schaffner (17), Campbell (2), Guignard (6), Hall (8), Murbeck (15), Cook (3), and others. Several other cases are mentioned by Coulter and Chamberlain (4).

The nucleus of the micropylar chamber gradually changes its position, moving toward the middle of the chamber, and soon afterward produces a great many free nuclei (figs. 46, 47), around which walls are subsequently formed, beginning at the micropylar end. This mode of development of the endosperm corresponds to the third type in Hegelmaier's (9) classification. Twelve chromosomes, that is, the $3x$ number, were often counted in these nuclear divisions. The nucleus of the antipodal chamber also moves toward the center of that chamber, and increases in size, but does not undergo division for a long time (figs. 46, 47). The antipodal chamber elongates like a haustorial tube, extending to the chalazal extremity of the ovule, sometimes becoming exceedingly curved.

Figs. 48 and 49 illustrate two parts of the same embryo sac; the endosperm tissue is seen to be fully formed in the micropylar chamber, while the antipodal chamber is still uninucleate.

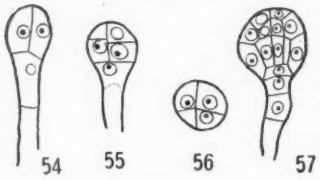
A large amount of starch is present in the embryo sac, as was also observed by GUIGNARD (7) (*Cestrum*), D'HUBERT (5) (Cactaceae), WEBB (18) (*Astilbe*), and LLOYD (12) (*Galicium*). This is observable not only a little before fertilization, but more especially after fertilization has occurred (figs. 43, 44, 46). Fig. 46 shows starch not only in the micropylar and antipodal chambers, but also even in the egg cell. It is evident that the starch grains in the micropylar chamber are always larger than those in the antipodal chamber. These starch grains are naturally closely related to those in the nutritive jacket. I have already mentioned that jacket cells loaded with starch grains may protrude into the sac. Sometimes one gains the impression that the starch grains have entered the sac through the destruction of the thin walls of the jacket cells. Such a direct transfer of starch, however, is hardly to be credited, partly because there are many fewer grains in the sac than in the jacket, but mainly because the walls of the jacket cells seem to be composed of very resistant material, since they persist for a long time apparently intact. In the *V. hastata* material I found occasionally an entire absence of starch grains in the jacket cells, and in such cases the development of the embryo sac is always remarkably retarded, and the egg apparatus is absent (fig. 50).

The further development of the endosperm is the same as in *Sagittaria*, described by SCHAFFNER (17). While the micropylar chamber is becoming filled with walled endosperm tissue through free nuclear division, the enlarged nucleus of the antipodal chamber still remains undivided. Sometimes it divides once or twice (fig. 51), forming two or three free nuclei which enlarge enormously. Meantime the endosperm tissue continues to develop, finally extending from the micropylar chamber into the antipodal chamber, forcing the large cell which occupies the antipodal chamber up to the antipodal end. At about this time the antipodal cells disintegrate (fig. 52). The large cell at the antipodal end of the chamber gradually diminishes in size, and finally disappears.

In COULTER and CHAMBERLAIN'S book (4) it is stated that "the endosperm is said to develop only in the antipodal chamber in *Loranthus*, Vacciniaceae, Verbenaceae, etc." This statement should be corrected as far as it concerns the various species of *Verbena* which I have studied.

DEVELOPMENT OF EMBRYO

The proembryo divides in two by a transverse wall and remains without further change for a long time (fig. 49). It then elongates, with accompanying divisions, reaching a condition like that illustrated in fig. 53, where it is a filament of varying length, consisting of several cells. The apical cell of the filament then divides longitudinally (fig. 54), followed by another longitudinal and a transverse division in either order, resulting in an octant stage (figs. 55, 56).



FIGS. 54–57.—*V. hastata*: successive stages of development of embryo; fig. 56, apical view of stage in fig. 55; ×400.

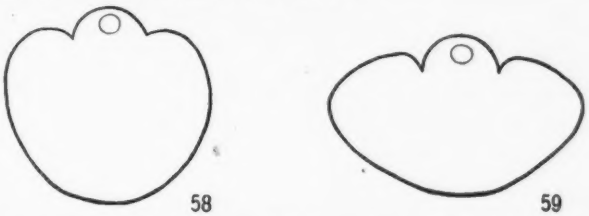
The dermatogen, periblem, and plerome layers are next differentiated in the embryo (fig. 57), which now occupies the end of a long suspensor. The appearance is identical with that of *Capsella*.

Relationship of intermediate forms

COOK, comparing two species of *Sagittaria*, *S. variabilis* and *S. lancifolia*, says: "With such striking external differences one would naturally expect equally interesting internal differences, but to my surprise I found the development of the embryo sac and embryo of *S. lancifolia* practically the same as had been described by SCHAFFNER for *S. variabilis*." I was equally surprised on comparing the forms of *Verbena*. I selected as the intermediate form for comparison with the original species the type designated in the earlier part of this paper as no. 5 (see fig. 5), because it is one of the most abundant of the intermediates and because it seemed to be halfway between *V. stricta* and *V. hastata*. In the following account the morphological and cytological characters of this intermediate are compared with those of the three species.

The flowering period of *V. angustifolia* comes earlier than that of *V. stricta*, *V. hastata*, and the intermediate form between them, so that the last three flower at the same time. For this reason one would expect that intermediate forms between *V. angustifolia* and the other two species would be rather rare, while those between *V. stricta* and *V. hastata* would be more common, if these intermediate forms are really hybrids. As a matter of fact, the relative abundance of the intermediates corresponded to the expectation.

The young ovule of *V. hastata* at the stage in which the megaspore mother cell first makes its appearance (fig. 15) is rounded (fig. 58), while that of the other three forms is somewhat flattened, as indicated in fig. 59. The young ovule of the intermediate form is therefore similar to that of *V. stricta*.



58 59

FIGS. 58, 59.—Diagrammatic outline of young ovule: fig. 58, *V. hastata;* fig. 59, other 3 forms.

The size of the mature embryo sac varies considerably within each species owing to individual variations, but an approximate comparison of its size at the same stage in the four forms can be made without difficulty. The following table gives the average length of 12 embryo sacs of the four forms at three different stages.

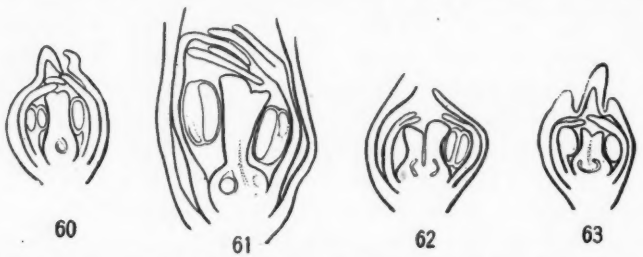
TABLE II

Name	*V. angustifolia*	*V. stricta*	Intermediate form between *V. stricta* and *V. hastata*	*V. hastata*
Fig. 26 stage.....	0.260 mm.	0.225 mm.	0.185 mm.	0.185 mm.
Fig. 51 stage.....	0.500	0.460	0.390	0.310
Fig. 56 or 57 stage	0.460	0.540	0.360	0.340

The breadth of the sac in all cases is about 0.02–0.03 mm. The figures show that with regard to the length of the embryo sac the intermediate form resembles *V. hastata* more than it does *V. stricta*.

At the time of the first mitosis of the microspore mother cell the flower buds of the 4 forms are in different stages of development. As shown in figs. 60–63, the buds of *V. angustifolia* and *V. hastata* are in a relatively young stage when this event occurs, those of *V. stricta* in a much later stage, and the intermediate form at a stage between these two. In respect to this character, then, the latter occupies an intermediate position.

As described in a preceding section, tetrad formation occurs in *V. angustifolia* in two different ways, with or without persistence of a rim of cytoplasm from the mother cell. In *V. stricta* the cytoplasm always persists in this manner, forming, even at the first mitosis of the microspore mother cell, a deeply stained border



FIGS. 60–63.—Comparison of florets at time of first mitosis in pollen mother cells: fig. 60, *V. angustifolia;* fig. 61, *V. stricta;* fig. 62, intermediate form between *V. stricta* and *V. hastata;* fig. 63, *V. hastata;* ×35.

around the central portion where the mitosis is occurring (figs. 64, 65). In *V. hastata* no such cytoplasmic border is ever formed around the microspores, but all of the cytoplasm of the mother cell is utilized in the production of the pollen grains. The intermediate form is like *V. hastata* in this regard (figs. 66–68).

V. angustifolia has 8 chromosomes as the $2x$ number. A late prophase and metaphase of the first reduction division in this species are shown in profile view in figs. 69 and 70. The other 3 forms have 12 chromosomes as the $2x$ number. A metaphase of *V. stricta* and an early anaphase of the intermediate form from the side and end are illustrated in figs. 71–74. I regret that in *V. hastata* I was unable to find just the same stage to compare with these, as all of my material of this species is either a little too early or too

late. It is safe to conclude, however, that 12 is also the $2x$ number for this species, since in the early telophase of the first division (fig. 75) 6 chromosomes are clearly present at each pole of the spindle. I have further often counted 12 chromosomes in all of the forms except *V. angustifolia* in the anaphase stage in young locular cells of anthers, and 18 chromosomes, the $3x$ number, in the endosperm cells. The behavior of the chromosomes of the intermediate form in mitosis is entirely normal, and like that of the original species. No such abnormalities as were described by ROSENBERG (**16**) in *Drosera* hybrids can be recognized.

Owing therefore to the unfortunate fact, which could not be foreseen, that both of the original species selected for comparison with a form intermediate between them have the same number of

FIGS. 69–75.—Mitosis of pollen mother cell: figs. 69, 70, *V. angustifolia;* figs. 71, 72, *V. stricta;* figs. 73, 74, intermediate form between *V. stricta* and *V. hastata;* fig. 75, *V. hastata;* ×1500.

chromosomes, cytological observations upon them do not serve to settle the question as to whether the intermediate form is a hybrid or not. It is clear that the intermediate form does not differ cytologically from the original forms, and that its mitotic behavior is entirely normal. These facts, if they have any significance at all, tend to suggest that the intermediate is not a hybrid, but rather a mutant of one or the other of the original species. This could be determined only by breeding it through several generations and observing whether its characters are fixed or not.

Cytological studies of the forms intermediate between *V. angustifolia* and the other two species might have yielded more definite results, because it differs from them in the number of its chromosomes. Unfortunately I did not collect any material from these forms, as they are relatively rare.

Summary

Several intermediate forms were found between three species of *Verbena* which grow on Stony Island, *V. angustifolia* Michx., *V. stricta* Vent., and *V. hastata* L., which can be arranged taxonomically between the three species in question. Embryological and cytological studies were made on the three species and on one of the forms intermediate between *V. hastata* and *V. stricta* in order to determine the genetic nature of the intermediate.

From the cytological point of view, nucellar cap, nutritive jacket, and chambered embryo sac are pointed out as the characteristic features of these forms. The reduced number of chromosomes is 4 in *V. angustifolia* and 6 in the other three.

It was not possible to decide from the cytological studies whether the intermediate form is a hybrid or not, since both of the original species from which it might be supposed to have sprung were found to have the same number of chromosomes. The chromosome behavior of the intermediate was like that of the two species and entirely normal. Some of its developmental characters are intermediate and some are similar to either *V. stricta* or *V. hastata*.

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EXPLANATION OF PLATES VI–IX

Figs. 10–17, 27, 54–63, 69–75 are in the text; all the others in the plates. All drawings were made with an Abbé camera lucida at table level. Figs. 11–17, 27, and 60–63 were drawn with Zeiss compensating ocular no. 4 and Spencer 16 mm. objective; figs. 18–25, 28–41, and 64–68 with Reichert ocular no. 18 and Spencer 4 mm. objective; figs. 26 and 42–53 with Zeiss compensating ocular no. 4 and Bausch and Lomb 1/12 oil immersion objective; figs. 69–75 with Reichert ocular no. 18 and Bausch and Lomb 1/12 oil immersion objective. Text figures reduced one-half, plates nearly two-thirds in reproduction. The original magnification will be specified for each figure in the plates.

PLATE VI

All figures reduced five-twelfths.

FIG. 1.—*Verbena angustifolia* Michx.

FIG. 2.—Taxonomically intermediate form between *V. angustifolia* Michx. and *V. stricta* Vent.

FIG. 3.—*V. stricta* Vent.

FIGS. 4–6.—Taxonomically intermediate forms between *V. stricta* Vent. and *V. hastata* L.

FIG. 7.—*V. hastata* L.

FIGS. 8, 9.—Taxonomically intermediate forms between *V. hastata* L. and *V. angustifolia* Michx.

PLATE VII

FIGS. 18–25 magnified 700 diameters; fig. 26 magnified 800 diameters; figs. 22 and 25 are *V. hastata;* all the others *V. angustifolia.*

FIG. 18.—Details of ovule outlined in fig. 15, showing megaspore mother cell.

FIG. 19.—Nucellus of older ovule.

FIGS. 20, 21.—Megaspore mother cell nucleus dividing into two (20), and four (21).

FIG. 22.—Growth of fertile megaspore and its encroachment on sterile cells; nucellus cells somewhat stretched.

FIG. 23.—Embryo sac with 2 nuclei.

FIG. 24.—Embryo sac with 4 nuclei, reconstructed from 4 sections.

FIG. 25.—Embryo sac with polar nuclei in contact.

FIG. 26.—Details of a part of ovary outlined in text fig. 27, showing mature embryo sac invested by jacket; proteid-like substance in space between ovule and carpel.

PLATE VIII

FIGS. 28–41 magnified 700 diameters; figs. 42–45 magnified 800 diameters; figs. 42, 45 are *V. stricta;* all the others *V. angustifolia.*

FIG. 28.—Longitudinal section of young anther showing sporogenous cell row and surrounding layers.

FIGS. 29, 30.—Transverse and longitudinal sections through an older anther, showing granular and mostly binucleate tapetal cells: fig. 29, cells of middle layer, also granular; fig. 30, some rows of pollen mother cells, with nuclei in synapsis.

FIG. 31.—Three pollen mother cells in first division; tapetal cells with 2 nuclei.

FIG. 32.—Two pollen mother cells in anaphase of first division.

FIG. 33.—Early telophase of second division in pollen mother cell.

FIGS. 34, 35.—Tetrad formation; some cytoplasm of mother cell concerned in wall formation.

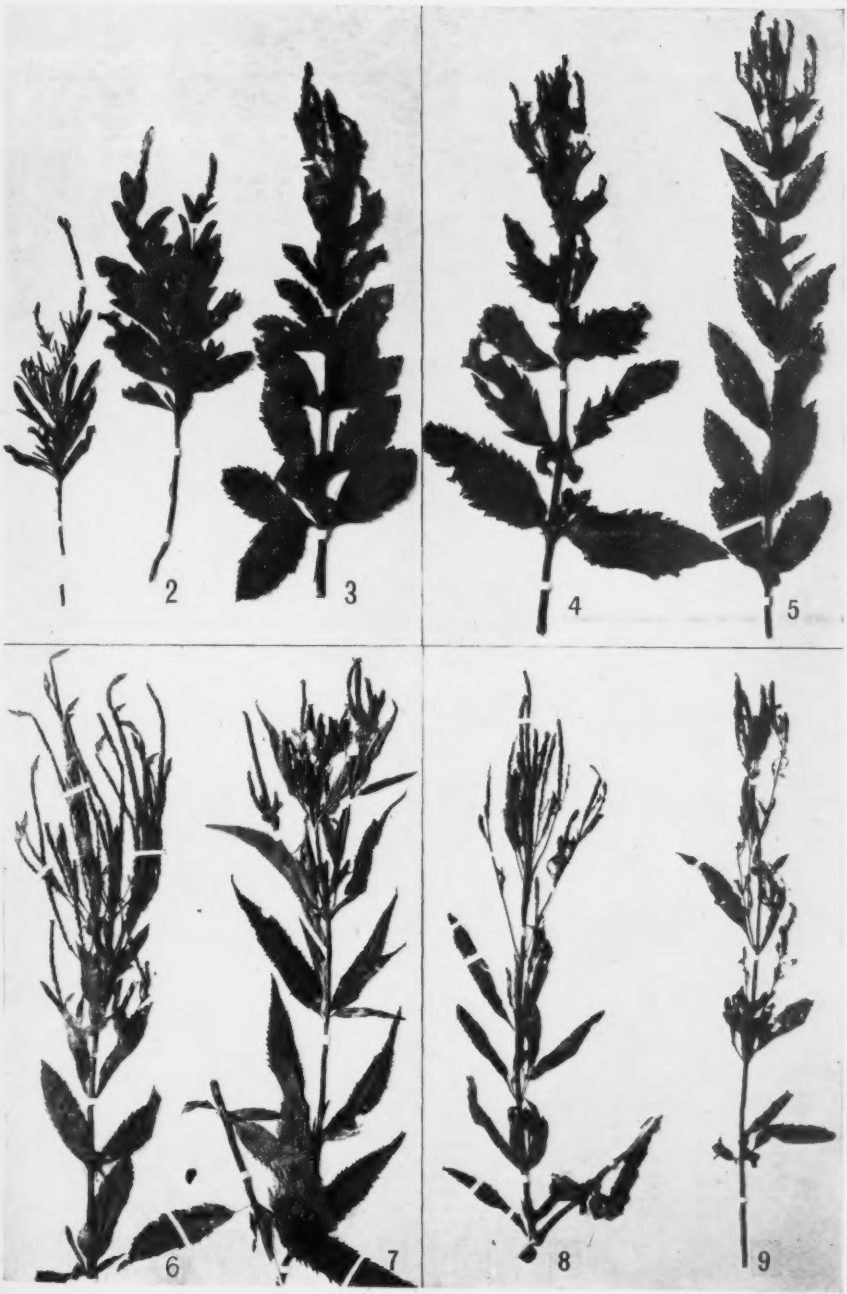
FIG. 36.—Tetrad formation; cytoplasm of mother cell not concerned in wall formation.

FIGS. 37–41.—Successive stages of development of pollen grain: fig. 39, pollen with starch grains; fig. 40, pollen with large vacuole; fig. 41, pollen with vegetative and generative nuclei.

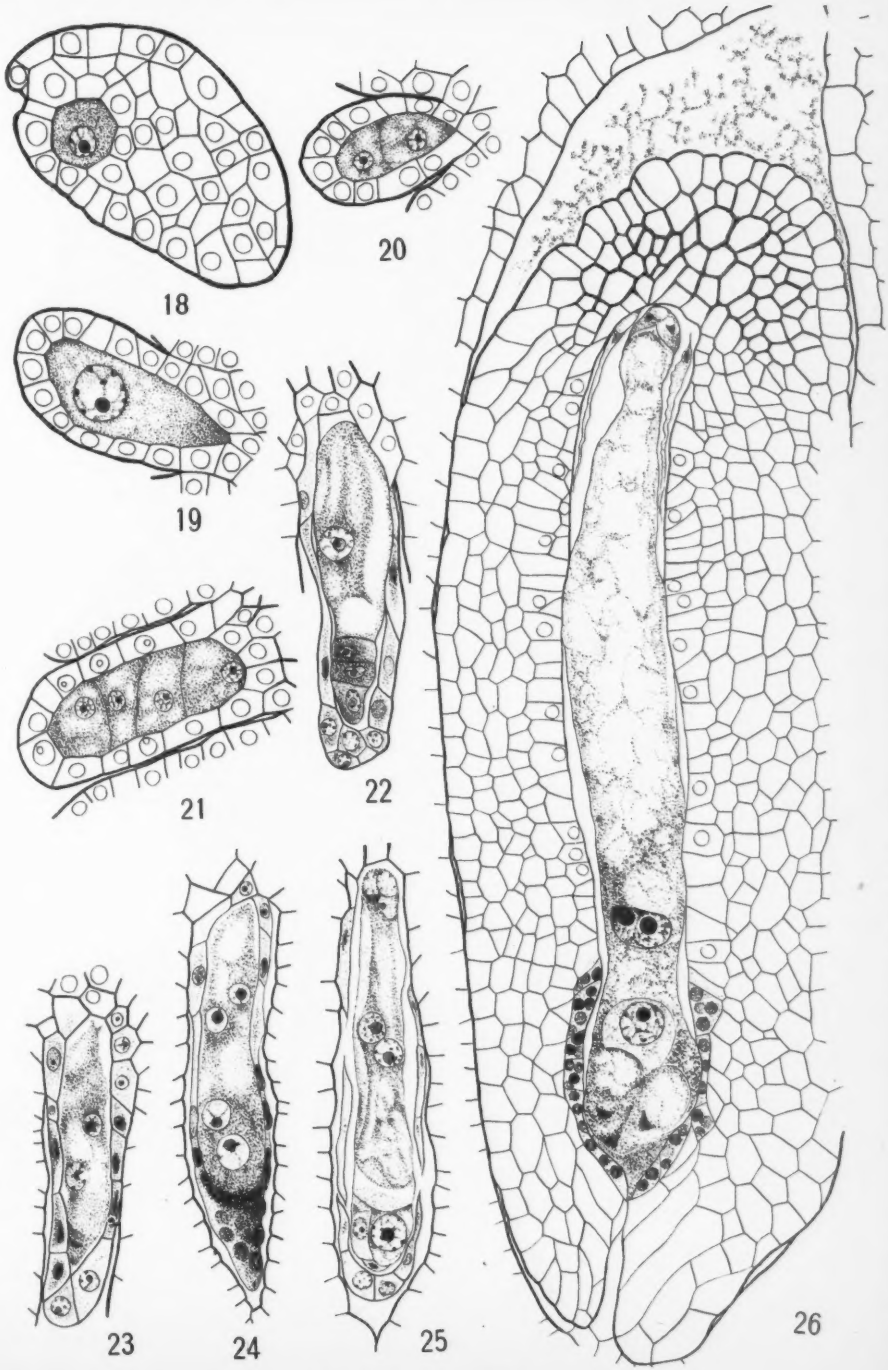
FIG. 42.—Pollen tube just thrusting itself through nucellar cap.

FIGS. 43, 44.—Fertilization: fig. 43, male nuclei fusing with egg and endosperm nucleus; pollen tube and starch grains shown.

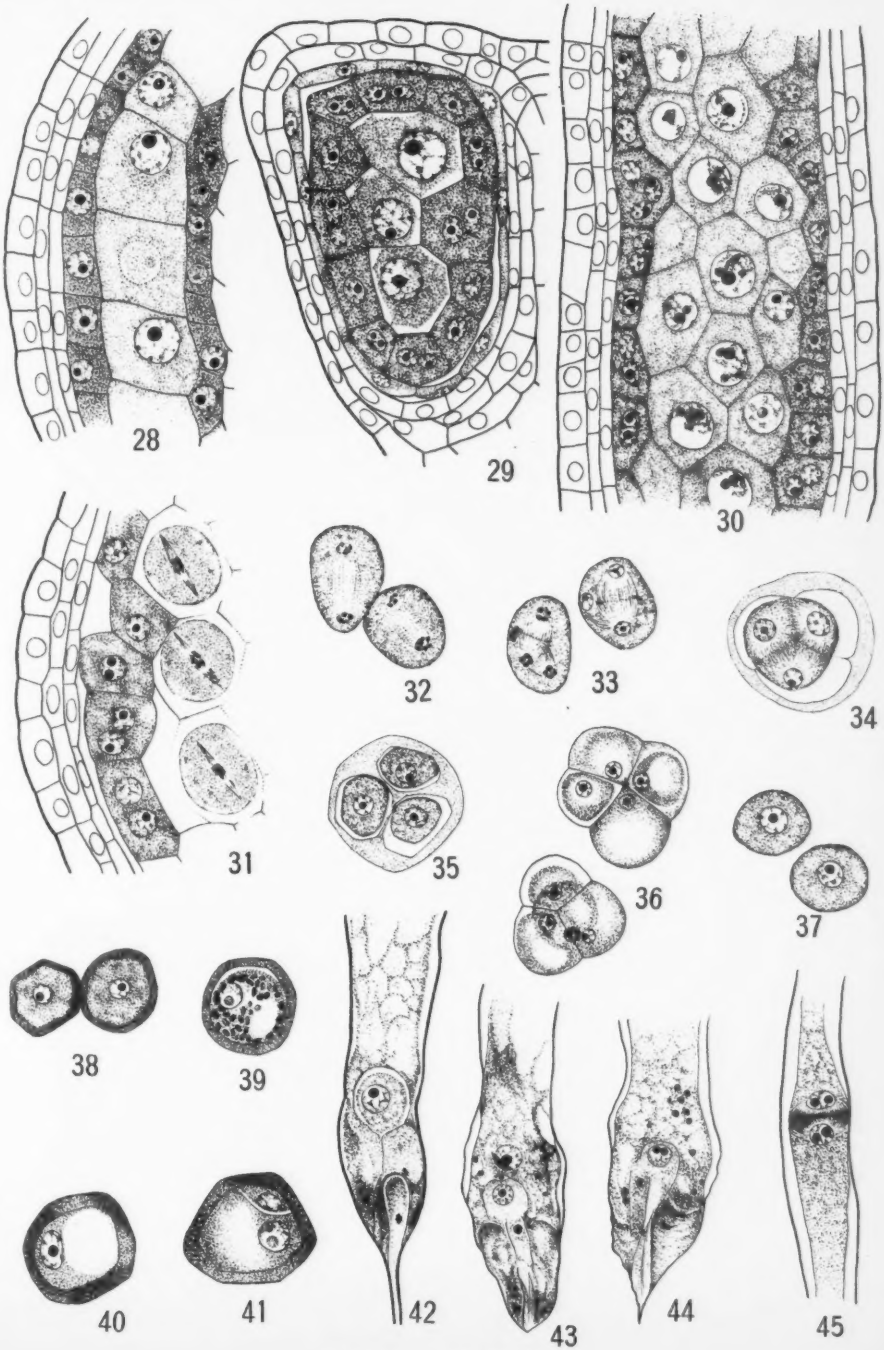
FIG. 45.—First division of primary endosperm nucleus followed by wall formation.



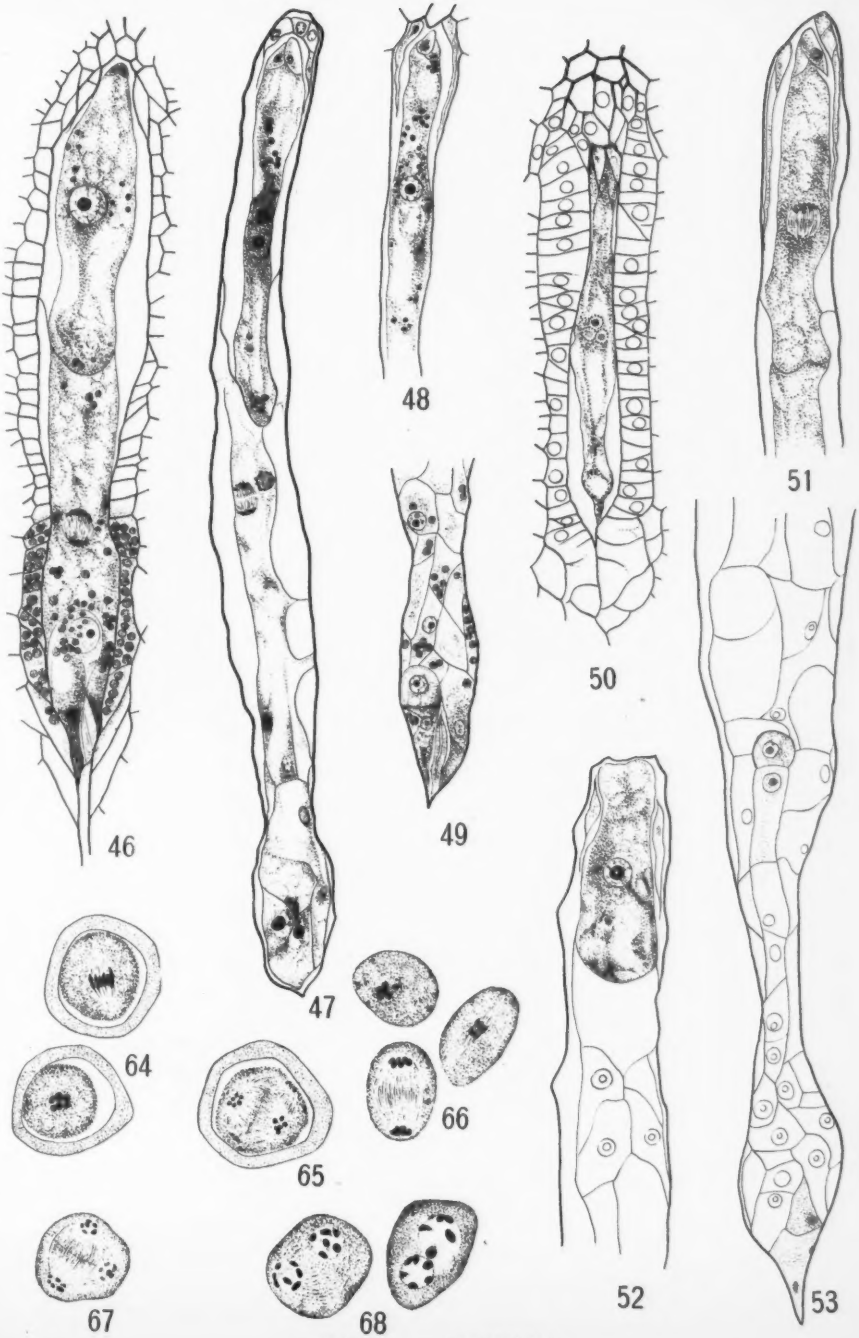
KANDA on VERBENA



KANDA on VERBENA



KANDA on VERBENA



KANDA on VERBENA

PLATE IX

FIGS. 46–53 magnified 800 diameters; figs. 64–68 magnified 700 diameters; figs. 50, 68 are *V. hastata;* figs. 64, 65, *V. stricta;* figs. 66, 67, intermediate form between *V. stricta* and *V. hastata;* all others are *V. angustifolia.*

FIG. 46.—Embryo sac separated into micropylar and antipodal chambers: nucleus in micropylar chamber just in mitosis; reconstructed from 4 sections.

FIG. 47.—Embryo sac in which endosperm tissue is developing from micropylar end; single large undivided nucleus with 2 nucleoli in antipodal chamber.

FIGS. 48, 49.—Two portions of one embryo sac: fig. 48, antipodal chamber still 1-celled; fig. 49, micropylar chamber filled with tissue.

FIG. 50.—Embryo sac retarded in development by absence of starch in jacket; only 3 nuclei in center.

FIG. 51.—Mitosis of endosperm nucleus in antipodal chamber.

FIGS. 52, 53.—Two parts of more advanced embryo sac: fig. 52, antipodal part with one large resting cell; fig. 53, micropylar part with filamentous embryo.

FIGS. 64, 65.—Pollen mother cell in reduction division: fig. 64, metaphase of first division; fig. 65, early telophase of second division.

FIGS. 66, 67.—Pollen mother cells: fig. 66, metaphase and telophase of first division; fig. 67, telophase of second division.

FIG. 68.—Pollen mother cell in telophase of second division.

A CHEMICAL ANALYSIS OF SUDAN GRASS SEED

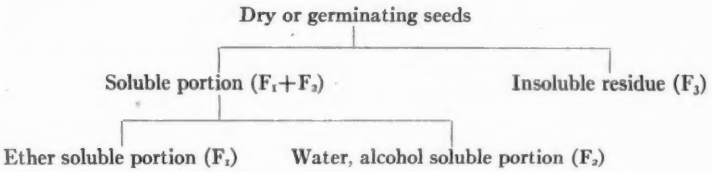
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 258

F. M. SCHERTZ

(WITH ONE FIGURE)

The method as here outlined was originally taken from the methods of WALDEMAR KOCH,[1] who employed it in the analysis of brain tissues. The method was then further modified by F. C. KOCH,[2] of the department of physiological chemistry, University of Chicago, where the work was chiefly on animal tissues. The method was again modified to meet the needs of plant tissues.

Outline of method



Fraction 1 (F_1) is the ether soluble portion; fraction 2 (F_2) is the portion soluble in alcohol or water; and fraction 3 (F_3) is the portion which is insoluble in ether, water, or alcohol. The dry seeds were ground finely before making the extraction, while the germinating seeds were ground in a mortar as finely as possible. The material was then placed in the extraction cups and extracted for 4 hours. A 1-hour extraction with ether was then made and the ether extract was added to the alcohol extract. The residue was dried, ground in a mortar, and then a water extraction was made. This water extraction and the residue was then made up to 70 per cent alcohol and again extracted with 95 per cent alcohol for 12 hours. In some cases this extraction was found to be insufficient,

[1] KOCH, WALDEMAR, Methods for the quantitative chemical analysis of animal tissues. Archives Neurology and Psychiatry 4: 11. 1909; also Jour. Amer. Chem. Soc. 31: 1329–1364. 1909.

[2] Outline for the analysis of tissues as prepared by F. C. KOCH.

and consequently the extraction was prolonged for another 12 hours or more. The extraction was conducted at the boiling point of the solvent, using the KOCH extractor.

F_1 and F_2.—All of the alcohol, water, and ether extracts were added to each other, and then the whole was rapidly evaporated down to a thick syrup on the water bath. It was then transferred to a vacuum desiccator and dried until nearly a constant weight was obtained. This took from one to three weeks. The air in the desiccator was changed once or twice daily. This gave the weight of F_1 and F_2. The dry mixture of F_1 and F_2 was now extracted with anhydrous ether; this extract was F_1, and the residue was F_2. The evaporating dish plus F_2 was dried and again weighed, giving the weight of F_1 by difference, and also the weight of F_2. The ether extract F_1 was divided into two portions, one portion being used for the determination of sulphur and phosphorus, and the other for nitrogen. The residue was dissolved or suspended in 70 per cent alcohol and made up to a volume of 1000 cc. Of this, 50 cc. was used to determine the total sugars; 100 cc. for ash and for solids; 200 cc. for nitrogen; 100 cc. for free reducing sugars; and 550 cc. for sulphur and phosphorus.

F_3.—F_3 was then dried at 105° C. in an electric oven to nearly a constant weight. The whole was then pulverized thoroughly and fractions of it, ranging from 0.5 to 2.0 gm., were used for the determination of sulphur, phosphorus, nitrogen, total carbohydrates, ash, and crude fiber.

Moisture was obtained by difference. Nitrogen was estimated by means of the Kjeldahl method as modified by Gunning and Arnold. The nitrogen was multiplied by 6.25 to give the protein. Sulphur was estimated by the fusion ($Na_2CO_3+KNO_3$) method, precipitated, and weighed as $BaSO_4$. The filtrate from the sulphur determination was used and the phosphorus was determined from it by the Neumann-Pemberton method, by titration. Organic matter was determined by taking the weights of the ash F_2 and F_3 from the dry weights of F_2 and F_3 respectively. Sugars were estimated by the Bertrand volumetric method in connection with the Munson and Walker tables. Total reducing sugars were found by adding 10 cc. of HCl (sp. gr. 1.125) for every 100 cc.

of water used with the sample, and then boiling on a reflux condenser for 2.5 hours. They were then estimated as glucose.[3] Crude fiber was determined after the method in Bulletin no. 107, Bureau of Chemistry. 1912.

Analysis of unhulled dry seeds

The air dry weight of the seeds used in each case was 25 gm. The seed analyzed was that of Sudan grass (*Holcus halepensis sudanensis* [Piper] Hitchcock or *Andropogon halepensis sudanensis* Piper). In each case two analyses were made and the results, together with the average of these two, are given in table I. The hulled seed was 70.62 per cent of the whole seed by weight, hence the hulls were 29.38 per cent of the whole seed by weight.

Analysis of seeds after germination

An analysis was made of the unhulled seeds which were kept in the refrigerator for 16 days at a temperature ranging from 8 to 20° C. A small percentage of the seeds showed signs of sprouting. In each case 25 gm. of seed were used.

This study was undertaken with the hope of discovering some of the early changes which take place on germination, and also because Sudan grass has promise as a forage grass. In comparing the unhulled dry seeds with the unhulled germinated seeds, it was found that the weight of F_1 remained constant, F_2 lost 2 per cent, and F_3 lost 3 per cent on germination. The protein in F_1 decreased, while that of F_2 increased somewhat. The total protein content of the germinated seeds increased about 1 per cent, due to the building of protein from the reserve substances. No change of importance was noted regarding the sulphur or phosphorus content. The ash of F_2 increased slightly at the expense of the ash of F_3. The amount of organic matter in F_2 decreased 1.5 per cent, while that of F_3 decreased 3 per cent; or a total loss of organic matter of about 5 per cent due to respiration. The greatest changes were found in the sugars. The total reducing sugar of F_2 decreased 2 per cent, free reducing sugar decreased slightly, and the total carbohydrates decreased about 9 per cent. The decrease in sugar-like products

[3] MATHEWS, ALBERT P., Physiological chemistry. 2d ed. New York. 1916.

TABLE I

	I	II	Average
Moisture		14.05	13.95
Weight of F_1		3.69	3.69
" " F_2		9.54	9.54
" " F_3	72.92	72.72	72.82
Total		100.00	100.00
		Protein*	
F_1		0.02	0.02
F_2		1.23	1.23
F_3	5.44	4.96	5.20
Total		6.20	6.45
		Sulphur	
F_1		0.02	0.02
F_2		0.05	0.05
F_3	0.07	0.09	0.08
Total		0.16	0.15
		Phosphorus	
F_1		0.004	0.004
F_2		0.06	0.06
F_3	0.20	0.24	0.22
Total		0.304	0.284
		Ash (inorganic matter)	
F_2		0.65	0.65
F_3	4.61	4.56	4.58
Total		5.21	5.23
		Organic matter	
F_2		8.89	8.89
F_3	68.31	68.16	68.24
Total		77.05	77.13
		Sugars	
F_2 total reducing		2.39	2.39
F_2 free reducing		0.96	0.96
F_3 carbohydrates	58.59	62.36	60.47
Total		64.75	62.86
		Crude fiber	
F_3	5.12	4.77	4.95

* The whole seed was analyzed and it gave a total for protein of 7.23 and 7.38 per cent.

TABLE II

RESULTS OF ANALYSIS OF HULLED DRY SEEDS*

	I	II	III	Average
Moisture	12.53	.....	12.76	12.46
Weight of F_1	4.24	.....	4.72	4.48
" " F_2	6.56	.....	7.87	7.22
" " F_3	76.67	76.19	74.65	75.84
Total	100.00	.....	100.00	100.00
	Proteins			
F_1	.....	.....	0.01	0.01
F_2	1.06	.....	1.07	1.06
F_3	7.28	7.26	7.54	7.36
Total	.....	.....	8.62	8.43
	Sulphur			
F_1	0.01	.....	0.01	0.01
F_2	0.05	.....	0.08	0.06
F_3	0.27	0.21	0.17	0.22
Total	0.33	.....	0.26	0.29
	Phosphorus			
F_1	.....	.....	0.002	0.002
F_2	0.08	.....	0.10	0.09
F_3	0.26	0.22	0.25	0.24
Total	.....	.....	0.352	0.332
	Ash			
F_2	0.82	.....	0.82	0.82
F_3	1.41	1.36	1.26	1.34
Total	2.23	.....	2.08	2.16
	Organic matter			
F_2	5.74	.....	7.05	6.40
F_3	75.26	74.83	73.39	74.50
Total	81.00	.....	80.44	80.90
	Sugars			
F_2 total reducing	0.34	.....	.....	0.34
F_2 free reducing	0.27	.....	0.26	0.27
F_3 carbohydrates	67.29	64.72	66.48	66.16
Total	67.63	.....	.....	66.50
	Crude fiber			
F_3	1.08	0.98	.....	1.03

* Air dry weight of the seeds used in each case was 25 gm.

TABLE III

	I	II	Average
Moisture absorbed	48.22	45.72	46.97
Moisture	18.34	19.12	18.73
Weight of F_1	3.25	3.94	3.60
" " F_2	8.03	7.58	7.80
" " F_3	70.38	69.36	69.87
Total	100.00	100.00	100.00
	Proteins		
F_1	0.01	0.01	0.01
F_2	2.20	2.66	2.43
F_3	5.10	4.93	5.02
Total	7.31	7.60	7.46
	Sulphur		
F_1	.....	0.01	0.01
F_2	0.05	0.05	0.05
F_3	0.16	0.13	0.15
Total	.....	0.19	0.21
	Phosphorus		
F_1	0.002	0.001	0.001
F_2	0.06	0.08	0.07
F_3	0.21	0.23	0.22
Total	0.272	0.311	0.291
	Ash		
F_2	0.85	.....	0.85
F_3	4.54	4.49	4.52
Total	5.39	.....	5.36
	Organic matter		
F_2	7.19	.....	7.19
F_3	65.84	64.87	65.36
Total	73.03	.....	72.55
	Sugars		
F_2 total reducing	.....	0.49	0.49
F_2 free reducing	0.40	0.33	0.37
F_3 carbohydrates	48.84	53.24	51.04
Total	.....	53.73	51.53
	Crude fiber		
F_3	5.54	4.63	5.08

was about 11.5 per cent, due to respiration. Crude fiber remained practically constant.

When the hulled dry seeds were compared with the unhulled dry seeds, it was found that the weight of F_1 was 1 per cent greater in the former, and it was 2 per cent greater in the latter for F_2, while F_3 of the former was about 3 per cent greater. The proteins of

TABLE IV

UNHULLED DRY SEEDS

Material	I	II	Average
Free reducing sugars	1.10	0.93	1.02
Sucrose-like sugars	1.94	2.43	2.19
Total reducing sugars	3.32	2.71	3.02
Total carbohydrate F_3	60.00	59.60	59.80
Total	63.32	62.31	62.82*
	Unhulled seed grown at room temperature		
Free reducing sugars	1.02	0.96	0.99
Sucrose-like sugars	1.54	1.39	1.47
Total reducing sugars	3.24	3.25	3.24
Total carbohydrate F_3	43.36	45.88	44.62
Total	46.60	49.13	47.86
	Unhulled seed grown in refrigerator		
Free reducing sugars	0.89	0.75	0.82
Sucrose-like sugars	1.64	1.34	1.49
Total reducing sugars	2.69	2.69	2.69
Total carbohydrates F_3	43.51	43.93	43.72
Total	46.20	46.62	46.41

* Ten gm. of seed were hydrolyzed for 2.5 hours and gave a total carbohydrate of 65.30 per cen t

F_1 and F_2 were about the same, but the protein of F_3 of the hulled dry seeds was more than 2 per cent greater. The ash of F_2 was slightly more in the hulled dry seeds, while the ash of F_3 was over 3 per cent greater in the unhulled seeds; hence a greater part of the ash was in the hulls. The organic matter of F_2 of the unhulled dry seeds was 2.5 per cent greater, while in F_3 it was 6 per cent less. The free reducing sugars were slightly greater in the unhulled seeds,

the total reducing sugars were 2 per cent greater, while the carbohydrates were over 6 per cent less. Five times as much crude fiber was found in the unhulled seeds.

A further analysis of the sugars was then made. Two samples of 25 gm. each of the dry seed were analyzed for sugars alone. Two samples of 25 gm. each were grown at room temperature (16–24° C.) for 3 days, and two other samples were grown in the refrigerator for 32 days. The seeds in each case were extracted as indicated into the two portions F_2 and F_3. F_2 was then evaporated down and made up to a volume of 500 cc., of which 100 cc. was used for the determination of total reducing sugars; three 50 cc. samples for the inversion of cane sugar by weak hydrolysis at 67–69° C. for 10 minutes; and the remainder was used for free reducing sugars. All of the F_3 was hydrolyzed for 2.5 hours by adding 300 cc. water and 30 cc. hydrochloric acid (sp. gr. 1.125). From small portions of this the total sugars of F_3 were determined.

From table IV it is seen that when the seeds germinate the sucrose-like sugars decreased about 1 per cent, while there was a decrease in the total carbohydrates of about 15 per cent.

TABLE V

SUDAN GRASS COMPARED WITH OTHER SEEDS

Seeds	Water	Protein	Fat	N-free extract	Crude fiber	Ash	Sugar
Triticum sativum	13.37	10.93	1.65	70.01	2.12	1.92	2–7
Hordeum sativum	12.95	10.01	1.87	67.88	4.23	3.06	6–7
Secale cereale	13.37	11.19	1.68	69.36	2.16	2.24	2–3
Zea Mays	13.32	9–10	4–5	68–69	1.6–2.7	1.60	1.5–3.7
Sorghum saccharatum	14.58	9.44	3.18	68.55	2.54	1.71	.....
Oryza sativa hulled	13.17	8.13	1.27	75.50	0.88	1.03	1–2
Oryza sativa unhulled	.....	.....	2.00	.....	.....	3.57	.....
Avena sativa	12.8	10.25	5.27	59.68	9.97	3.02	2–5
Holcus halepensis sudanensis unhulled	13.94	6.44	3.69	75.74*	4.95	5.24	2.39†
Holcus halepensis sudanensis hulled	12.47	8.43	4.48	71.43*	1.03	2.16	3.44†
Unhulled germinated seed in refrigerator	18.72	7.46	3.60	59.78*	5.08	5.36	2.69†
Sudan grass seed (Kansas)‡	10.47	13.69	3.81	63.63	5.38	3.09	.....

* 100−(protein+ether extract+ash+moisture+crude fiber).

† Total reducing sugars as dextrose.

‡ THOMPSON, G. E., Sudan grass in Kansas. Kansas Agric. Exper. Sta. Bull. 212. 1916.

It is of interest to compare these results with those of some other workers. KJELDAHL, working on barley seed, found about 4.7 per cent cane sugar in the green malt and 1.1 per cent in the ungerminated barley. O'SULLIVAN found in ungerminated barley 0.8–1.6

and in malt 2.8–6.0 per cent cane sugar. These results on Sudan grass gave in each case less than 1.0 per cent of cane sugar, figuring the reducing sugar as cane sugar.

Compared with other grasses[4] it is very similar to *Sorghum avenaceum*, which gave the following results: ash 5.63, protein 3.29, cellulose 36.7, and fat 1.67 per cent. Of the ash, 1.5–3.0 per cent was CaO, P_2O_5, MgO, and SO_3.

Catalase activity

In each case 0.2 gm. (dry weight) of the seed was used. The results are given in cubic centimeters of oxygen set free in 10 minutes at 20° C.

Dry seeds		Seeds at room temperature 3 days
Hulled seeds	Unhulled seeds	Unhulled seeds
13.8	15.5	54.0
17.2	17.0	65.2
		68.2
15.0	16.25	
		62.4

Seeds in refrigerator 31 days	
Unhulled seeds	Unhulled seeds
45.0	46.0
50.8	50.6
45.6	50.0
47.1	49.0

The seeds which were grown in the refrigerator showed less catalase activity; part of this lessened activity may be due to the lowered temperature, but part of it undoubtedly was also due to the fact that the seeds at room temperature had grown slightly more than those in the refrigerator.

Microchemistry

A brief microchemical analysis was undertaken in order to locate the materials in the tissue of the seed, as well as to get an idea of how much was present (fig. 1).

Practically all of the cell walls gave the blue color reaction with 75 per cent H_2SO_4 and iodine, except the two small regions of the integument at each end of the caryopsis. With phloroglucin-HCl a cherry red color was observed in the pericarp integument near

[4] WEHMER, C., Die Pflanzenstoffe. Jena. 1911.

the micropylar end of the caryopsis. With acetone and a drop of concentrated HCl a red color was noted on the pedicel, and especially was the red prominent in the whole pericarp integument. This indicated strongly the presence of methyl pentosan, and perhaps araban and xylan. No callose was observed in any of the tissues. With ruthenium red, the pericarp integument and the cell membranes of the starchy endosperm gave slight tests, while the scutellum, plumule, plumule sheath, radicle, and root shoot gave a strong reaction, indicating the presence of much pectic substance. Small particles in the cells also gave a pectose reaction. The phloroglucin-HCl tests showed only traces of lignin, if any, present in the pedicel and in the glume. Upon heating the tissues with concentrated HNO_3 and concentrated $KClO_3$, ceric acid was observed to issue from the tissues of the pericarp integument. Suberin was present here.

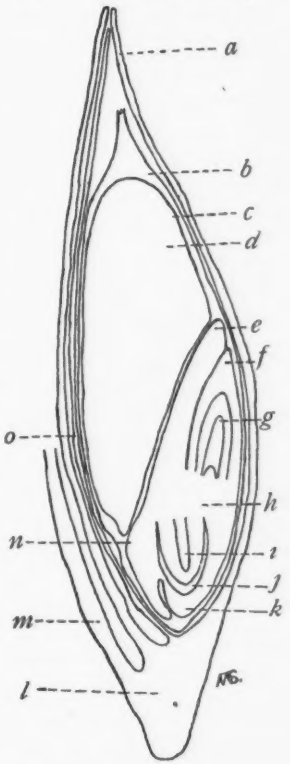


FIG. 1.—Longitudinal section of grain of Sudan grass: *a*, glume; *b*, pericarp; *c*, aleurone layer; *d*, endosperm; *e*, scutellum; *f*, coleoptile; *g*, plumule; *h*, embryo node; *i*, radicle; *j*, root cap; *k*, coleorhiza; *l*, pedicel; *m*, basal seta; *n*, glandular layer of scutellum; *o*, lodicule.

All cells of the embryo, and especially the cells of the embryo at the micropylar end, were rich in oil. The fat-containing cells of the endosperm stained heavily with Sudan III. Also, the epithelial layer had some fat present. The whole of the embryo became red when treated with concentrated H_2SO_4, and later took a greenish hue. Hence, phytosterol was thought to be present in the embryo, and also in a portion of the seed coat at the micropylar end of the caryopsis.

Silicon was found in the pericarp, as was shown by heating a dry section of the tissues with phenol. Tannins were found in the glumes and in the outer coats of the seeds, where red and purplish colors were observed, which were probably due to the oxidized tannins.

Two sizes of starch grains were found. The endosperm cells were filled with large sized starch grains, while the pericarp integument, the pedicel, and the basal seta had smaller grains in them.

Neither dextrin nor glucose was present in the embryo or in the endosperm, but considerable was present in the hulls. Amylodextrin was found in all of the endosperm cells in rather large quantities. The layers of the cells of the caryopsis outside of the fat-containing endosperm cells all gave a positive reaction for glucose when treated with copper tartrate and sodium hydroxide.

TABLE VI

MICROCHEMISTRY OF SUDAN GRASS SEED

Part of seed	Cellulose	Pentoses	Pectic substances	Lignin	Suberin	Fat	Phytosterol	Tannin	Starch	Glucose	Amylodextrin
Pedicel	+*	+	.....	+	.....	.....	.....	.....	+	.....	.....
Glume	+	.....	.....	+	.....	.....	.....	+	.....	++	.....
Basal seta	.....	.....	.....	.....	.....	.....	.....	.....	+	.....	.....
Lodicule	+	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Pericarp	+	++	+	.....	+	.....	+	+	+	+	.....
Aleurone layer	.....	.....	.....	.....	.....	++	.....	.....	.....	.....	.....
Endosperm	+	.....	+	.....	.....	.....	.....	.....	++	.....	++
Epithelial layer	.....	.....	.....	.....	.....	+	.....	.....	.....	.....	.....
Scutellum	+	.....	++	.....	.....	+	+	.....	.....	.....	.....
Embryo node	+	.....	++	.....	.....	+	+	.....	.....	.....	.....
Radicle	+	.....	++	.....	.....	++	+	.....	.....	.....	.....
Coleorhiza	+	.....	++	.....	.....	++	+	.....	.....	.....	.....
Plumule	+	.....	++	.....	.....	+	+	.....	.....	.....	.....
Coleoptile	+	.....	++	.....	.....	+	+	.....	.....	.....	.....

* +=present; ++=present in large amount.

In conclusion, I wish to acknowledge my obligations to Professor WILLIAM CROCKER, under whom this work was done, for his advice and valuable criticisms; to Dr. S. H. ECKERSON for her untiring interest and advice relative to the microchemistry; and to Professor F. C. KOCH for his helpful suggestions in the methods of chemical determinations involved.

BUREAU OF PLANT INDUSTRY
WASHINGTON, D.C.

BRIEFER ARTICLES

WILLIAM GILSON FARLOW

(WITH PORTRAIT)

With Dr. FARLOW, whose death occurred on June 3, 1919, after a short illness, there passes not only a unique personality, but one whose preeminence in his special field was such that to no one else could the title of cryptogamic botanist, in the broader sense, be so justly applied. Apart from his extensive familiarity with other branches of botany, it is doubtful if anyone has ever approached him in his knowledge of the non-vascular plants as a whole, a knowledge so comprehensive as well as so detailed, that in matters relating to most of the larger groups his opinion was rightly regarded as that of an expert.

Gifted with an extraordinarily retentive memory, exceptional ability, keen discernment, and sound judgment; appreciating the necessity for a wide and thorough training for his work; possessing, also, sufficient means with which to avail himself of opportunities, many of which were such as come only to the pioneer, he was able to accumulate books, collections, and other material needs for the execution of his purposes. His equipment thus included intellectual and material factors which combined to make him one of the foremost figures in the botanical world.

Dr. FARLOW'S interest in botany had already developed during his undergraduate days at Harvard, and his natural fondness for the subject was fostered and developed by his contact with ASA GRAY, by whose

advice, after graduation, he studied medicine in preparation for a scientific career. Receiving his Doctor's degree in 1870, he became GRAY'S assistant, and had the privilege of teaching and studying with him for two years. Although, during this association, he gained a comprehensive knowledge of the vascular plants, his preference for the non-vascular types, and especially the algae, was already apparent, since it is with the latter that his first two papers, "Cuban seaweeds" (1871) and "List of the seaweeds or marine algae of the south coast of New England" (1871–1872), are concerned.

GRAY'S interests, being primarily systematic, were naturally impressed on Dr. FARLOW, and the former evidently contemplated the conversion of his pupil into a collaborator who might in a measure do for the lower cryptogams what he had himself done for the flowering plants, even to the point of preparing a manual. Although no portion of this program was carried out, the preparation of a textbook of cryptogamic botany was in Dr. FARLOW'S mind more or less constantly, until the idea was finally abandoned in the early nineties. It was partly with this in view that he was advised by GRAY, after serving two years as his assistant, to visit Europe, come in personal relations with European botanists, acquire a knowledge of their methods of working and of teaching, and above all to learn as much as possible of the lower forms, especially the fungi and lichens. He therefore sailed for Liverpool in June 1872, and went first to Scandinavia, where he saw, among others, the elder FRIES, as well as ARESCHOUG and AGARDH and their herbaria. He continued his journey as far as St. Petersburg, where he desired to see the algae in the Ruprecht Herbarium. Although he also traveled in Germany, Switzerland, France, Italy, and England, meeting many well known botanists, he passed most of his time at Strassburg in DEBARY'S laboratory, spending also some weeks in an intensive study of the lichens with Dr. J. MULLER at Geneva, and of the algae with BORNET and THURET at Antibes. DEBARY was then professor of botany and regent of the German University, which had replaced the French Académie after the close of the Franco-Prussian War, and was reputed to know more about the fungi, their morphology and development, than anyone else in the world. Dr. FARLOW was thus able to fill this, the most serious gap in his equipment, and to acquire, among other things, a good foundation in general plant anatomy. Here he came in contact with SCHIMPER, then an old man and the most distinguished member of the scientific faculty, Graf SOLMS, recently appointed ausserordentlich professor, and various students attracted by DEBARY'S courses: STAHL,

ROSTAFINSKI, SOROKIN, GILKINET, LINDSTEDT, and others. He was strongly influenced by the personality of DEBARY himself, his wide knowledge, ability, earnestness, and high ideals of care and accuracy in scientific work. The training which he thus acquired served as a fitting complement to that which he received from ASA GRAY, the impress of whose systematic predilections was thus tempered by DEBARY's very different point of view. Work of a taxonomic or even of a general nature was not encouraged in the latter's laboratory, and he was regarded by Dr. FARLOW as somewhat narrow in his conception of the scope and extent of the preparation desirable in the preliminary training of a botanist. He was not himself, however, restricted to a special topic until more than a year after he entered the laboratory, when DEBARY, having observed the vegetative development of a fern sporophyte from the prothallus, turned the subject over to him for investigation. The resultant paper, on "An asexual growth from the prothallus of *Pteris cretica*," published in the *Botanische Zeitung* and elsewhere, attracted wide attention and interest, and, although it was at first attacked from all sides, rendered his name familiar to botanists everywhere.

His reputation was thus well established when he returned to America in the summer of 1874, and was appointed to an assistant professorship at Harvard, the first special provision in this country for instruction in cryptogamic botany. For some years he was stationed at the Bussey Institution, where his work dealt largely with the economic aspects of mycology, and where he may be said to have laid the foundations of American phytopathology. During this period of 5 years his published papers on fungi were largely devoted to destructive parasites, such as the black knot, grape mildew, onion smut, etc., although he did not neglect the marine algae, and published several articles on the algal impurities of water supplies.

In 1879 he was transferred to Cambridge as professor of cryptogamic botany, a position which he continued to occupy until his death, after a service on the Harvard faculty of 45 years. He was thus able to devote himself to the Farlow Herbarium, the nucleus of which was the well known Curtis Herbarium, purchased during his absence in Europe, and of his unrivaled library of books, papers, and journals relating to cryptogamic botany; the development of instruction in different branches of the subject, as well as of productive investigation on his own part and that of his students.

In 1883 he instituted the numbered series of "Contributions from the Cryptogamic Laboratory of Harvard University," which, up to the

time when he retired from active teaching in 1896, included the titles of some 40 papers, which, with the exception of the four first numbers written by himself, represent original work accomplished by his students. Among the latter were included B. D. HALSTED, WILLIAM TRELEASE, J. E. HUMPHREYS, W. A. SETCHELL, K. MIYABE, H. M. RICHARDS, and other well known names of American botanists. His own publications during this period were numerous, and included, for example, "Monograph of the Gymnosporangia," "Marine algae of New England," "Host index of fungi," etc. It is greatly to be regretted that his *magnum opus*, on selected species of fleshy fungi, for which an edition of very beautiful plates was printed long before his death, has been left uncompleted.

Although he continued a member of the Harvard faculty until his death, he withdrew from teaching in the year just mentioned, giving attention occasionally to advanced students in whose work he felt a special interest, devoting himself chiefly to the care and increase of the herbarium and of his library, as well as to the supervision of the extensive "Bibliographical index of American fungi," the first part of which, prepared in collaboration with A. B. SEYMOUR, was published by the Carnegie Institution in 1905. At the same time he kept up his botanical reading, about which he was hyperconscientious, and which was varied and extensive, being by no means limited to matters relating to cryptogams alone; while he also carried on a voluminous correspondence, sparing neither time nor trouble to assist those in search of advice or information as to identities, synonymy, or literature.

Throughout his life Dr. FARLOW was an indefatigable collector, and his activity of body and keen eyesight, which were little impaired by age, combined with his long experience and wide and exact knowledge, enabled him to detect a host of new, rare, or interesting forms. His annoyance at encountering unrecognizable, and in numberless instances undoubtedly new, forms, was often very amusing. He had so little patience with species makers that he himself described but a very small percentage of the novelties that came in his way. Of those who make a profession of this type of botanical activity he once said to his class, "If a difference can be *imagined*, it is a new species; if one can be *seen*, it is a new genus." A number of new genera and species were none the less named in his honor, of which he laughingly asserted that "they were almost all bad."

Dr. FARLOW'S attainments, his rare ability and learning, commanded the respect of all who came in contact with him, and were given recogni-

tion by the bestowal of honorary degrees (LL.D. by Harvard, Wisconsin, and Glasgow, and Ph.D. by Upsala), as well as by his election to membership in the National and Paris Academies of Science, the American Philosophical Society, the American Academy of Arts and Sciences, the Linnaean Society of London, and various other scientific bodies in this country and abroad. His good judgment, keen sense of humor, originality, and faculty for interesting presentation never failed to render any public deliverance of his a memorable event.

There are few that have been brought into close relations with him as students, or in scientific work, whose standards and ideals he did not fundamentally influence; while those who had experienced his unfailing kindness, thoughtfulness, and sympathetic interest not only regarded him with the honor and respect due to his character and attainments, but with a personal feeling of obligation and affection.—ROLAND THAXTER, *Harvard University.*

CURRENT LITERATURE

NOTES FOR STUDENTS

Mitosis in Osmunda.—Cytologists are familiar with the two outstanding views, associated respectively with the names of GRÉGOIRE and FARMER, regarding the method of chromosome reduction. According to the first view the doubleness of the spirem of the early heterotypic prophase, unlike that of the somatic prophase, is due to a lateral conjugation of threads representing entire chromosomes to form bivalents which are separated at the heterotypic mitosis, a new split functioning in the homotypic. According to the second view the doubleness is due to a split as in somatic mitosis; bivalents are formed by a conjugation of segments of this double spirem which separate in the first mitosis, while the original split functions in the second. A very complete statement of this latter interpretation has been given by Miss DIGBY[1] in a new account of mitosis in *Osmunda*.

In all the archesporial divisions, including the last, the chromosomes undergo a longitudinal splitting during early telophase. The homogeneous daughter threads become beaded as the split between them widens, and with many small connecting strands eventually form a faint resting reticulum which bears many small granules, and in which the limits of the individual chromosomes are indistinguishable. Most of the chromatin is collected in three or more nucleoli. In the succeeding prophase the reticulum resolves itself into a number of thin beaded linin threads; these run in parallel pairs and are regarded as the two reassociating halves of the chromosomes split in the preceding telophase. As the association becomes closer, the material of the threads is progressively concentrated, until it takes the form of a double spirem which segments into split chromosomes. These are separated into their component halves at anaphase and undergo a new splitting during telophase. Nuclei may go from the telophase of the last premeiotic division directly into the heterotypic prophase, or may pass through an intervening resting stage.

In the heterotypic prophase the reticulum gives rise to beaded "threads" which become more uniform spirems with a distinct parallelism, just as in the archesporial prophases. At this stage occurs synizesis, during which the reassociation of the parallel threads to form "filaments" is completed. From the contraction emerges a thick double spirem homologous with the double

[1] DIGBY, L., On the archesporial and meiotic phases of *Osmunda*. Ann. Botany 33:135–172. *pls. 8–12. fig. 1.* 1919.

spirem of the somatic prophase; the doubleness is believed to be the result of splitting in the last premeiotic telophase, and not to a conjugation of entire chromosomes. This double univalent spirem, which is more or less conspicuously beaded according to the fixing agent employed, is soon thrown into loops and the split becomes obscured. During the succeeding stages segments of the spirem (the "filaments"), although originally arranged end to end before segmentation, conjoin laterally in pairs to form the bivalent chromosomes, a process which is consummated in the second contraction. It is here that the conjugation of entire chromosomes occurs, whereas at the first contraction (synizesis) daughter halves of chromosomes are reassociated. As the second contraction loosens, the bivalents shorten and thicken and take up positions near the periphery of the nucleus (diakinesis). Only rarely at this stage can the temporarily obscured split of each component of the bivalent be detected.

As the bivalent takes its place upon the spindle, its univalent components become somewhat disjoined, and each again reveals the fission which had its origin in the last premeiotic telophase and was most conspicuous in the spirem of the early heterotypic prophases, and which marks the line of separation for the homotypic mitosis. As the univalent passes toward the pole, its halves widen out along this line of fission, giving the V-form characteristic of the heterotypic anaphase. During early telophase each daughter half of the split univalent undergoes a new longitudinal fission; this is homologous with the split occurring in the somatic telophase; after being obscured it reappears in the homotypic anaphase and functions in the post-homotypic division. The telophasic transformation of the chromosomes occurs as described for the archesporial divisions, and during interkinesis the individual chromosomes are indistinguishable.

The homotypic division is regarded as essentially a continuation of the last premeiotic division, since the doubleness of the chromosomes of the homotypic prophase is held to be the same as that of the last premeiotic telophase; the heterotypic division is consequently an interpolated process effecting numerical reduction. Although the events of the homotypic division are "involved in some obscurity," they seem to be in the main as follows. The threads derived from the fission of the daughter halves of the univalent chromosomes in the heterotypic telophase reassociate in pairs and form a number of chromatic masses, which later take the form of loosely associated daughter univalents; these arrange themselves more or less independently on the spindle. During their anaphasic separation (along the line marked out in the last premeiotic telophase) the fission which had its origin during the close of the heterotypic mitosis, and which is to function in the post-homotypic mitosis, reappears. The chromosomes at telophase take the form of double beaded threads which establish the resting reticulum as in the archesporial mitoses.

Although in substantial agreement with the conclusions of FARMER and MOORE,[2] this interpretation of maturation is directly opposed to that of GRÉGOIRE[3] and YAMANOUCHI,[4] who hold that the double heterotypic spirem in *Osmunda* arises from a conjugation of thin threads, each representing an entire chromosome, as stated in the first paragraph of this review. The GRÉGOIRE school charges the FARMER school with a misinterpretation of the presynaptic stages, while the latter charges the former with a neglect of the second contraction stages. It is not to be denied that the view stated fully by Miss DIGBY has certain advantages: it allows one interpretation to be placed upon the double spirem in both somatic and heterotypic prophases, irrespective of the exact time at which the split originates, and it also helps to explain the sudden appearance of the split for the second maturation mitosis in the anaphase of the first.

This question, however, must be settled primarily by direct evidence. It is obvious that its solution depends upon the exact manner in which the telophasic transformation of the chromosomes and the derivation of the latter from the reticulum in prophase are accomplished. It is granted by both sides that the alveolar or reticulate condition in which the chromosomes are found in late telophase is continuous with the similar condition seen in the succeeding prophase. If, therefore, it is true (1) that the telophasic transformation (alveolization) represents a true splitting, and (2) that the early prophasic reticulate condition passes directly into the double spirem, it follows that this doubleness in every prophase is due to the fission which originated in the preceding telophase, as held by Miss DIGBY. Contrary to the statement of that author, however, workers on mitosis are not at all generally agreed that the evolution of the chromosomes is that stated in (1) and (2). In his investigation of somatic mitosis in *Vicia Faba* for the purpose of elucidating these points, the reviewer,[5] contrary to the findings of FRASER and SNELL,[6] FRASER,[7] and others, showed not only that the telophasic alveolization is too irregular to permit of its being regarded as a splitting, but also that the reticulate condition of the prophase, instead of developing directly into the definitive split, gives rise to simple thin threads in which a new split develops. From

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[2] FARMER, J. B., and MOORE, J. E. S., On the meiotic phases in animals and plants. Quart. Jour. Micr. Sci. **48**:489–557. *pls. 34–41.* 1905.

[3] GRÉGOIRE, V., La formation des gemini hétérotypiques dans les végétaux. La Cellule **24**:369–420. *pls. 2.* 1907.

[4] YAMANOUCHI, S., Chromosomes in *Osmunda*. BOT. GAZ. **49**:1–12. *pl. 1.* 1910.

[5] SHARP, L. W., Somatic chromosomes in *Vicia*. La Cellule **29**:297–331. *pls. 2.* 1913.

[6] FRASER, H. C. I., and SNELL, J., The vegetative divisions in *Vicia Faba*. Ann. Botany **25**:845–855. *pls. 62, 63.* 1911.

[7] FRASER, H. C. I., The behavior of the chromatin in the meiotic divisions of *Vicia Faba*. Ann. Botany **28**:633–642. *pls. 43, 44.* 1914.

this it cannot be concluded that in no form does the split develop directly from the early reticulate structures, or that the telophasic alveolization, although irregular, may not later become so equalized as to constitute the first stages of the split; but it does follow that it is quite unsafe to use the principle of telophasic splitting as a premise from which to draw the conclusion that the approximation of thin threads in the early heterotypic prophase represents the reassociation of the halves of a single split chromosome. Although it is well to emphasize the importance of the premeiotic telophase, the ultimate solution of this perplexing problem must be reached mainly through a more refined analysis of those prophasic changes which have led a long list of investigators to the conclusion that the early heterotypic association of threads represents a conjugation of entire chromosomes which separate at the heterotypic division. To the reviewer the figures so far given by the English cytologists do not prove the theory they advocate.—L. W. SHARP.

Carbohydrate economy of cacti.—A distinct contribution to our knowledge of the carbohydrates in plants in general, and in the succulents in particular, is the report of SPOEHR's investigations at the Desert Laboratory.[8] The methods employed give us what is probably the most complete analysis of the carbohydrates of a single plant tissue that we have, values for no less than 11 different groups of carbohydrates being ascertained, partly by direct determinations and partly by calculation.

The monograph is prefaced by a rather thorough discussion of carbohydrate metabolism in plants, and of the transformations of the carbohydrates under the influence of acid, alkali, oxidation, and enzymes, and of the energy relations of the products of these transformations. Then follows a description of the methods employed. *Opuntia phaeacantha* and *O. versicolor* furnished material for the studies. In preparing the tissues for carbohydrate analysis they were ground in a meat chopper and placed in an oven at 98° C. The precaution of DAVIS and DAISH of plunging the tissue into boiling alcohol was not deemed necessary. The disaccharides and polysaccharides were hydrolyzed by boiling with 1 per cent hydrochloric acid for 3 hours. All sugar determinations were made volumetrically with Fehling's solution. The pentoses were determined after fermenting away the hexoses with bakers' yeast.

The polysaccharides of the cactus are starch and xylan. The mucilage of *Opuntia* consists of 34.1 per cent d-glucose and 65.9 per cent l-xylose. Associated with it there is probably an acid. Glucuronic acid was found as a constituent of the sap. The formation of mucilage in special large cells could be watched under the microscope under certain conditions.

The relative abundance of the different groups of carbohydrates and also of water is profoundly affected by the seasonal variations of the external

[8] SPOEHR, H. A., The carbohydrate economy of the cacti. Carnegie Institution of Washington. Publ. 287. pp. 79. 1919.

conditions. From the cool and humid winter to the hot and dry fore-summer the water content of normal species of *Opuntia* may change from about 80 to 65 per cent, and then rise again to 83 per cent during the humid but hot mid-summer. "Low water-content and high temperatures are associated with: (1) increase of polysaccharides; (2) decrease of monosaccharides; (3) increase of pentosans. High water-content and lower temperatures are associated with: (1) decrease of polysaccharides; (2) increase of monosaccharides; (3) decrease of pentosans." The author points out the significant fact that "the greatest activity of the plant comes at a time when the content of monosaccharides and disaccharides is highest," in March and April, although he is careful to state that a relatively large supply of simple sugars is not the only prerequisite for growth, but is only one of many factors.

In an arid atmosphere the cut joints undergo considerable decrease in water content, while still remaining normal in appearance and activity. The loss of water by transpiration and evaporation is partly compensated for by the water formed in the combustion of sugars, and partly by the condensation of the simple sugars into polysaccharides. Under drought the former decrease, while the latter and the pentosans increase, in total amount. The author suggests that the great imbibitional force of the pentosans may prevent the use of water for hydrolytic processes, when water becomes scarce in the tissue. These phenomena are closely correlated with temperature effects, when the latter are studied independently of varying moisture supply. Enzyme equilibria are discussed in connection with these two factors.

During the night the succulents respire sugar to acids, principally malic. This is not accompanied by an accumulation of alcohol. In an oxygen-free atmosphere, however, there is much less acid formed, and a very considerable amount of alcohol produced. One molecule of malic acid furnishes two of carbon dioxide and one of ethyl alcohol. Under these anaerobic conditions more sugar is consumed per unit of energy than under aerobic conditions. This is accompanied by an increase in the water content of the tissue.

During starvation the joints of *Opuntia* maintain the same relative proportions of the various carbohydrates. This disproves the theory that the pentoses are waste products of metabolism, since then they would show an increase. The water relations of the tissue during starvation and during periods of feeding on sugar solutions are discussed at some length.

SPOEHR advances the theory that the pentoses may be formed from glucuronic acid by the loss of a molecule of carbon dioxide, and discusses the isomerism relations between the hexoses and the corresponding pentoses that would be formed through the intermediary of glucuronic acid.—J. J. WILLAMAN.

Transpiration in tropical rain forests.—The lack of experimental data as to the conditions of plant growth and activity in tropical rain forests is apparently leading to some desirable investigation. A notable contribution in this

field is by McLEAN,[9] who worked in the rich forests on the slopes of the hills near Rio de Janeiro, Brazil. This is a region of high average humidity, due to a rainfall of 111.2 cm., the heaviest downfall being during the warmer months, and to a very considerable amount of cloudiness upon days with no rainfall. Considerable climatological data are presented, and a graph of climatic favorability is devised by combining the four factors of temperature, rainfall, relative humidity, and sunshine. The curve of this graph seems to show that the year may be divided into a more and a less favorable period, the latter extending from June to December.

Atmospheric humidity is shown to be high, even outside the forest cover. Graphs are presented showing the relative range of humidity and temperature at various levels of the vegetation. The latter records prove that a dense layer of shrubs divides the forest into two strata, the lower possessing cooler and more humid conditions than the lighter and better ventilated regions above. The author believes that this lower stratum is the less favorable to vegetation, and to it his experimental work is confined.

Transpiration measurements by means of potometers give the water loss by leaves in the lower stratum of the forest always less than 0.4 of the evaporation from a free water surface exposed alongside the foliage. Experiments within the laboratory with similar temperature and humidity, but with higher illumination, are shown to give similar results. Many of the shade leaves possess an amount of cutinization that reduces cuticular transpiration to a very slight amount. Structural studies show the intercellular spaces of sun and shade leaves to be relatively 16.3 and 24.8 per cent, and these amounts correspond very closely to those found in Europe. The size and amount of stomata seem to be rather decidedly smaller than that found in typical mesophytes of temperate lands. The vascular strands of the shade leaves are much smaller in cross-structure than those of sun leaves. These data, and the fact that the author believes the power of root absorption to be low, make it probable that, even in the protected region of the lower interior of the forest, transpiration may for short periods decidedly surpass the low capacity of the plants to supply water. This is supposed to account for cutinization, semi-succulence, and other xeromorphic tendencies and features of the tropical forests.

Under such conditions of reduced transpiration, however, there is no shortage of mineral matter, but on the contrary the leaves from shaded and protected habitats show relatively a richer content than do those sun forms with a much higher transpiration rate. This would prove that here at least the absorption of mineral salts is quite independent of any transpiration current.

A study of the foliage proves the predominance of the lanceolate leaf form and a remarkable prevalence of nyctitropic folding, which, however, does not

[9] McLEAN, R. C., Studies in the ecology of tropical rain forests; with special reference to Brazil. I. Humidity. Jour. Ecol. 7:5–54. *pl. 1. figs. 21.* 1919.

seem to have a marked effect upon water loss. With the latter phenomenon is associated an abundance of pulvini.

The report is to be commended as an attempt to apply quantitative methods in an almost untouched field.—GEO. D. FULLER.

Heated soils.—JOHNSON[10] has done a very critical and exhaustive piece of work on the effect of heating soils at various temperatures on the germination of seeds and later growth of plants in such soils. The heating at 114–116° C. was done in an autoclave; at higher temperatures the heating was done with air-dry soils in dry ovens. The duration of heating was about 2 hours.

Soils heated at 100–115° C. gave temporary retardation of germination and seedling growth, followed later by a great increase in rate of growth. The extent of these varied greatly with the soil, seed, and plants used, and with other environmental conditions. The injury increased as the temperature rose up to 250° C. As the temperature rose above 250° C. the injury decreased until it was nil with heating at 350° C. or above. The time of recovery from the toxic effects was proportional to the intensity of the toxicity. Soils showed considerable variation in the degree of effect of heating. This variation cannot be explained on the basis of any one characteristic of the soil, but seems to result from a combination of a number of its characters.

Seeds varied in their sensitiveness. Lettuce and clover are very sensitive, and wheat, buckwheat, and flax are resistant. Gramineae and Cucurbitaceae are usually resistant, while Leguminosae and Solanaceae are more sensitive. There is great variation in the response of the growing plants. Heated soils that proved very injurious to some plants, as tomatoes, may be beneficial to others, as wheat. In general, but not always, there is a parallel between the sensitiveness of germination and of the later growth of the seedling. *Pyronema*, some other fungi, and some bacteria grow best in soils heated to 250° C., and fall off in growth rate with soils heated to higher or lower temperatures.

The ammonia content of soils is highest in those heated at 250° C., and diminishes as the temperature of heating rises or falls. The same is true of the concentration of the soil solution, so that there is a rough parallel between these characters of the soil and the degree of toxicity or later increased growth. Adsorptive capacity of the soil modifies the action of the toxic substance. In soil extracts the toxicity is more nearly correlated with the concentration of the ammonia. Additions of ammonia to soil produce effects similar to heating. The author believes the toxic action of heated soils is largely due to ammonia existing as ammonium carbonate. He thinks other factors are involved in so-called "chemical" injuries.

The toxic material in heated soils is volatile. It is also changed into non-toxic form when the soil is kept under conditions favoring growth of organisms. The latter is due to soil flora, and, contrary to PICKERING, does

[10] JOHNSON J., The influence of heated soils on seed germination and plant growth. Soil Science 7:1–87. 1919.

not occur under aseptic conditions. The amount of ammonia apparently may increase as organisms reduce the toxicity. The ammonia is assumed in this case to exist in delicate transition stages detected by analysis, but not in toxic form. The soils heated above 250° C. are supposed to be less toxic because much of the ammonia is volatilized by the high temperatures.

The author believes that heating to very high temperatures does not change the quality of the effects gained by heating at ordinary sterilizing temperatures, but merely makes these effects more marked by quantitatively intensifying them. His results, therefore, are valuable in elucidating the effects of sterilizing soils by heat.—Wm. Crocker.

Vegetation of an antarctic island.—Lying 600 miles southwest of New Zealand, 920 miles southeast of Tasmania, and 970 miles from the antarctic continent, Macquarie Island is in a position of great isolation. It is little more than a short range of mountains with peaks ranging from 900 to 1424 ft. in height, the length of the island being 21 miles and its breadth less than 4 miles. The hills descend rapidly toward the sea, forming bold headlands and precipitous cliffs with no harbors or sheltered bays. It possesses a remarkably equable temperature, the mean maximum being 43°.5 F. and the mean minimum 37°.9 F., while the extreme range is only 25°.8 F. A rainfall of 45 inches is distributed so that no month has less than 3 inches. Wind velocity is uniformly great, averaging 18 miles per hour.

It has an impoverished vascular flora of 30 seed plants, 3 ferns, and 1 lycopod. Concerning the origin and affinities of this flora, Cheeseman[11] decides that with the exception of 3 endemic grasses it dates back no farther than the last glacial epoch. Its repopulation was probably affected through the agency of birds, as half its species are common to New Zealand, 15 are found also in Fuegia or South Georgia, and a like number are circumpolar.

The vegetation is characterized by the entire absence of trees and shrubs. The conspicuous plant forms are the tussock grasses, principally *Poa foliosa*, the large leaved "Macquarie Island cabbage," *Stilbocarpa polaris*, an Araliaceous plant resembling a fine rhubarb, the cushion of *Azorella Selago*, globular mosses often 4 ft. across, and a purple flowered Composite, *Pleurophyllum Hookeri*, with long sage green leaves. Of these the tussock grass is most abundant, occupying much of the hillside slopes.—Geo. D. Fuller.

Journal of the Arnold Arboretum.—This new quarterly journal has been established to secure "the prompt publication of information about trees and shrubs collected at the Arnold Arboretum," which was a function of *Garden and Forest* (1887–1897). The first number (July 1919) includes the fifth paper of Camillo Schneider entitled "Notes on American willows" (pp. 1–32);

[11] Cheeseman, T. F., The vascular flora of Macquarie Island. Sci. Rep. Australian Antarctic Expedition of 1911–14. Series C. vol. 7. pt. 3. pp. 63. map. 1919.

"New species, varieties, and combinations from the herbarium and the collections of the Arnold Arboretum," by ALFRED REHDER (pp. 44–60); "A phytogeographical sketch of the ligneous flora of Korea," by E. H. WILSON (pp. 32–43); and the fifth paper by C. S. SARGENT entitled "Notes on North American trees" (pp. 61–65).—J. M. C.

Toxicity of alpha-crotonic acid.—Alpha-crotonic acid, in concentrations of 25–50 p.p.m., is very toxic to wheat plants. Its toxicity is markedly reduced by the phosphate radical, as SKINNER and REID[12] show by using it in water cultures of wheat with a three-salt medium varying according to the triangle system. The crotonic acid does not affect the relative absorption of any one salt, thus differing from some of the other toxic organic compounds studied in SCHREINER'S laboratory. The real nature of the antagonism is not known.—J. J. WILLAMAN.

New genera.—NAKAI[13] has described a new genus of Oleaceae (*Abeliophyllum*), found in Corea. It is an endemic and related to *Fontanesia* (Fraxineae), a monotypic oriental genus.

PENNELL[14] has described a new genus of Onagraceae (*Peniophyllum*), based on *Oenothera linifolia* as the type. In a conspectus of *Kneiffia* (*Oenothera*) he recognizes 13 species, 4 of which are described as new.—J. M. C.

Plant mucilage.[15]—The mucilage in cacti, mallows, tragacanth, and lilies arises in special large cells by hydrolysis of the cellulose wall, a hydrocellulose being an intermediate stage. These walls are not secondarily thickened. An account is given of the reaction of these mucilages to various stains.—J. J. WILLAMAN.

Germination.—RUSSELL[16] finds that the germination of camphor seeds in the commercial seed bed is greatly improved by removing the pulp. By pulping the seeds the increase in the number of seeds of transplantable size amounted to 60 per cent.—WM. CROCKER.

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[12] SKINNER, J. J., and REID, F. R., The influence of phosphates on the action of alpha-crotonic acid on plants. Amer. Jour. Bot. **6**:167–180. 1919.

[13] NAKAI, TAKENOSHIN, Genus novum Oleacearum in Corea media inventum. Bot. Mag. Tokyo **33**:153, 154. 1919.

[14] PENNELL, F. W., A brief conspectus of the species of *Kneiffia*, with the characterization of a new allied genus. Bull. Torr. Bot. Club **46**:363–373. 1919.

[15] LLOYD, F. C., Origin and nature of the mucilage in the cacti and in certain other plants. Amer. Jour. Bot. **6**:156–166. 1919.

[16] RUSSELL, G. A., Effect of removing the pulp from camphor seed on germination and the subsequent growth of the seedling. Jour. Agric. Research **17**:223–238. 1919.